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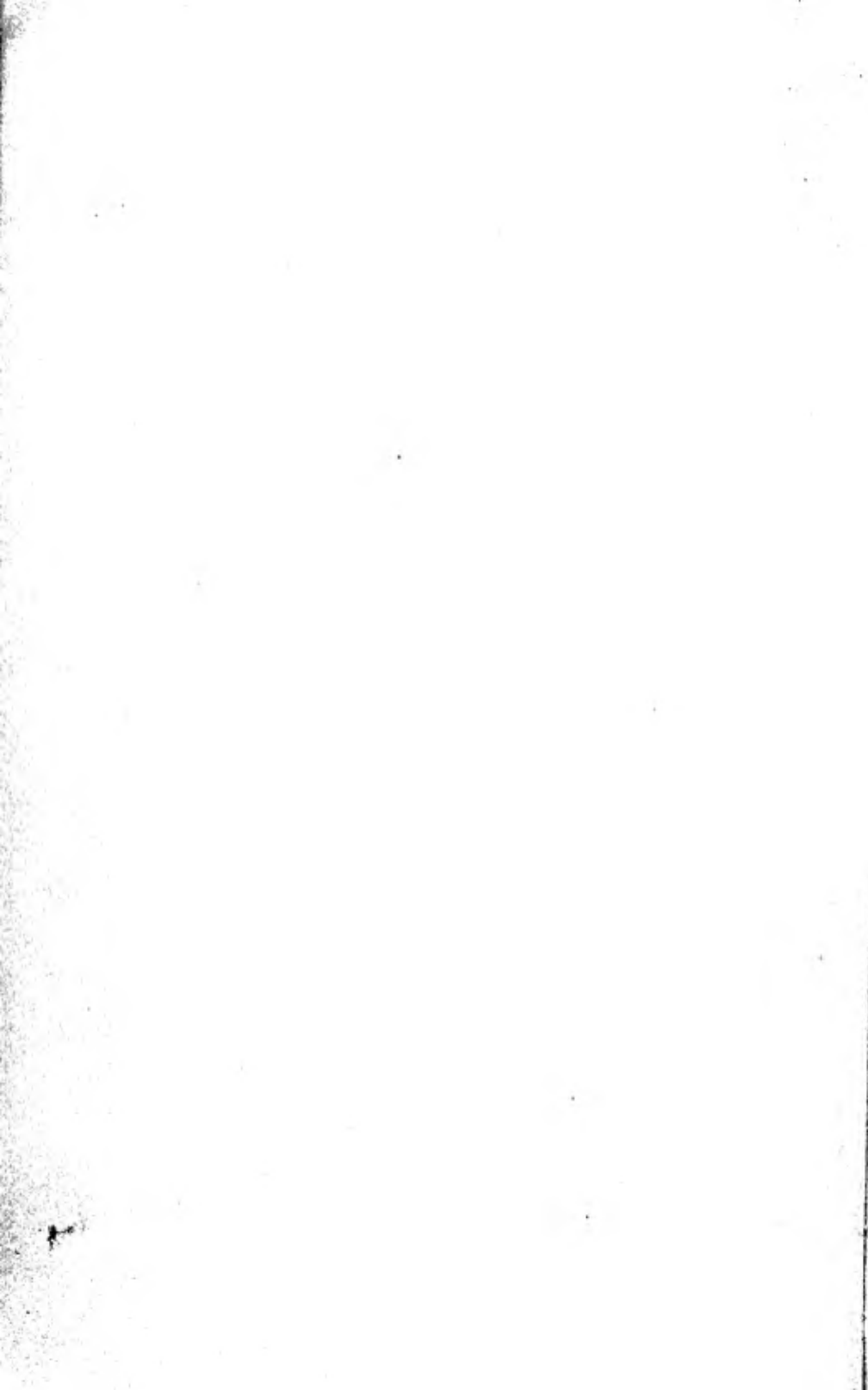
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CAMBRIDGE UNIVERSITY PRESS

C. F. CLAY, MANAGER

London: FETTER LANE, E.C.

Edinburgh: 100 PRINCES STREET



London: H. K. LEWIS AND CO., LTD., 136 GOWER STREET, W.C.

London: WILLIAM WESLEY AND SON, 28 ESSEX STREET, STRAND

New York: G. P. PUTNAM'S SONS

Bombay, Calcutta and Madras: MACMILLAN AND CO., LTD.

Toronto: J. M. DENT AND SONS, LTD.

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MORPHOLOGY AND ANTHROPOLOGY

A HANDBOOK FOR STUDENTS

BY

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FLORENCE, PARIS AND ROME

574.402

Due

SECOND EDITION

VOLUME I

B481(a)

Cambridge :
at the University Press

1915

First Edition: 1904

Second Edition: 1915

CENTRAL ARCHAEOLOGICAL
LIBRARY, NEW DELHI.

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Vol. 2 . . . 5 . . . 55

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PREFACE

AS the Introductory Chapter of this Volume deals with its aim and scope, any further exposition of these would be superfluous here. I hope that the materials thus brought together may prove useful to Students, particularly to those who combine Physical Anthropology with Human Anatomy in preparation for the Cambridge Natural Sciences Tripos. Inasmuch as such students are already familiar with anatomical terms, a general acquaintance with the significance of these has been assumed.

I believe the method indicated, however inadequately, herein to be the most profitable for anthropological work on the physical side: and I am convinced that upon some such basis only, can Physical Anthropology justify its claim to an independent place among the biological sciences.

The subject is now perfectly well defined and possesses so extensive a literature, that even a cursory review like the present volume has assumed proportions for which I must offer an apology. Several departments of the subject (and particularly Anthropometry) have merely been sketched in outline. A certain amount of repetition will be noticed, but is justifiable in view of the greater completeness conferred upon successive sections of the book. Most of the illustrations have been prepared by myself, in many instances from the original specimens or preparations.

Like other reviews, this cannot be other than a process of stocktaking. I have attempted to submit the main points in evidence up to date; yet however desirable an absolutely fixed standpoint may appear, it should not be forgotten that opinion must be adjustable to the requirements of every new fact, provided the latter be correctly observed and accurately recorded.

It is a pleasant duty to express my gratitude to those who have aided me; to my father, and to Professor Alexander Macalister, for ever-ready help and encouragement; to Professor Elliot Smith and to Dr Marett Tims, who kindly read parts of certain Chapters (*viz.* xv and vi), upon the subject-matter of which they are recognised as authorities of the highest competence.

The following have allowed the use of tables or information already published elsewhere:

Dr Ballantyne and Professor Cunningham of Edinburgh; Professor Eisler of Halle and Professor Le Double of Tours; Professors Parker and Haswell and Messrs Macmillan and Co.

I have endeavoured to render full acknowledgment, and hope that no omission has been made. References to literature are provided in the text: a special index contains the names of authors quoted. Where possible, I have attempted to verify or check statements by personal observation.



PREFACE TO THE SECOND EDITION

THE favourable reception accorded to the first edition of this book encourages the hope that, in its present form, it will meet with similar success. The whole of the first section has been rewritten. It has been enlarged so much that its publication as a separate volume seems advantageous. More than eighty illustrations have been added. The old illustrations have been furnished with reference lettering in an uniform style, and many of them have been re-drawn. This part of the work has been carried out largely by Mr Parker, formerly assistant to the late Mr Edwin Wilson, who also prepared several of the drawings. The patience and care of both these artists demand mention here. To the authorities and staff of the University Press I am indebted for advice, and to Mr J. Whittingdale of Downing College I owe the preparation of the General Index and the list of illustrations.

For photographs and for permission to copy or use clichés, I wish to thank more especially the following persons and institutions:

Dr Gregory (of the American Museum of Natural History), Professor Elliot Smith, Dr Charles Hose, Dr Brown, Dr Chalmers Mitchell, Professors Sherrington, Grünbaum, Schlaginhaufen, Schwalbe, Retzius, and Osborn; the Publishing Committees of the Royal Society and of the Royal Society of Medicine

(Odontological Section), the Macmillan Co., the London Electrotype Agency, Mr Heinemann, and the Editor of *L'Illustration* (Paris). Illustrations have also been borrowed from the publications of Professors Brodmann and Kramberger. Thus I have endeavoured to make full acknowledgement of the various sources of such illustrations as were not prepared in the form of sketches made by myself from dissections or skeletons.

W. L. H. D.

CAMBRIDGE

August 14, 1915

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ABBREVIATIONS

Anat. Anz.—*Anatomischer Anzeiger*.

Bibl. Zool.—*Bibliotheca Zoologica*.

Brit. Assoc. Report.—*Annual Report of the British Association for the Advancement of Science*.

Bull. de la Soc. d'Anthr. de Paris.—*Bulletin de la Société d'Anthropologie de Paris*.

J. A. P.—*Journal of Anatomy and Physiology*.

Jahr. der Anatomie.—*Jahresbericht der Anatomie*.

Kon. Ak. van Wet.—*Koninklijke Akademie van Wetenschappen*.

Linn. Trans.—*Transactions of the Linnaean Society*.

Linn. Soc. Journal.—*Journal of the Linnaean Society*.

Morph. Jahrbuch.—*Morphologisches Jahrbuch*.

Proc. Acad. Nat. Sc. Phil.—*Proceedings of the Philadelphia Academy of Natural Sciences*.

Proc. Anat. Soc.—*Proceedings of the Anatomical Society of Great Britain and Ireland*.

Proc. Camb. Phil. Soc.—*Proceedings of the Cambridge Philosophical Society*.

P. Z. S.—*Proceedings of the Zoological Society*.

Q. J. M. S.—*Quarterly Journal of Microscopical Science*.

Sitz. der Kais. preuss. Akad.—*Sitzungen der Kaiserlichen preussischen Akademie zu Berlin*.

Z. für M. und A.—*Zeitschrift für Morphologie und Anthropologie*.

Zool. Trans.—*Transactions of the Zoological Society*.

ADDENDUM

The multitude of synonyms applied to most of the Primates is a source of much confusion. Dr D. G. Elliot has published recently (1912) a magnificent work in which he has endeavoured to standardize the names to be applied to the various species. As the memoir in question (*A Review of the Primates*, Monographs of the American Museum of Natural History, Monograph Series, Vols. I-III) is of classical value, I have selected from it the names there given as the standard equivalents of those used in the present work. The list of synonyms is given in the following list:

<i>Name employed in text.</i>	<i>Name as given by Elliot.</i>
Anthropopithecus.	Pan.
Ateles.	Ateles.
Cheiromys.	Daubentonina.
Cynocephalus.	Papio.
Cercopithecus.	Lasiopyga.
Chrysothrix.	Saimiri.
Hapale.	Callithrix.
Macacus.	Pithecus.
Mycetes.	Alouatta.
Semnopithecus.	Pygathrix.
Simia.	Pongo.

The remaining names agree with those adopted by Dr Elliot. The substitution of *Pygathrix* for *Semnopithecus* demands special notice, for Dr Pilgrim (Records of the Geological Survey of India, Vol. XLV, Part 1) states in the present year (1915) that the official term should be *Presbytis*. Reference to Dr Elliot's work shews on the contrary that in point of priority, the term adopted by Dr Elliot (*Pygathrix*) is to be preferred.

CHAPTER I

INTRODUCTION

IN entering upon the study of the morphological aspects of Anthropology it is of the first importance to ascertain and realize the scope and limits of the subject. This is admittedly a somewhat difficult task, and the following account aims at giving some general information of an introductory nature.

The use of the term Anthropology is not modern, and when first employed¹ it referred in a general sense to human anatomy and physiology, the study of which was at the time referred to in a very elementary stage. In earlier days certain philosophers had been spoken of as anthropologists, and again in later times, *i.e.* in the 18th century, Anthropology was treated (by Kant and others) as a branch of philosophy, rather than of biology. The latter end of the 17th century was a most important epoch in the history of Physical Anthropology, using the term in the sense which it has now acquired and which will presently be explained. In the year 1699, Dr Edward Tyson, a member of Corpus Christi College, Cambridge, published under the auspices of the Royal Society a treatise entitled "*Orang-Outang, sive Homo Sylvestris. Or, the Anatomy of a Pygmie compared with that of a Monkey, an Ape, and a Man*".²

In 1501 by a German, Magnus Hundt, of Marburg.

² In this work we find described system by system and organ for organ the comparative anatomy of man and a "Pygmie." Upon the evidence thus provided is based a discussion of the relations of the two forms, the differences as well as the resemblances of the two animals are taken into due consideration, and the author sums up to the effect that "our Pygmie is no Man, nor yet the Common Ape, but a sort of animal between both." The descriptions, the illustrations, and the skeleton of the "Pygmie" (now in the Natural History Museum, S. Kensington), shew that it was an immature Chimpanzee.

Without entering upon detailed criticism of this work, it will suffice to remark that it constitutes a most remarkable anticipation of modern methods of research, and still serves as a model for investigations into the structure of Man and Apes (Fig. 1). Nevertheless although so important in these respects the work was not described as one on Anthropology, nor is it certain that Tyson made use of the term in connection with it.

The 18th century in turn affords several notable names in the history of Physical Anthropology. The chief contributors to

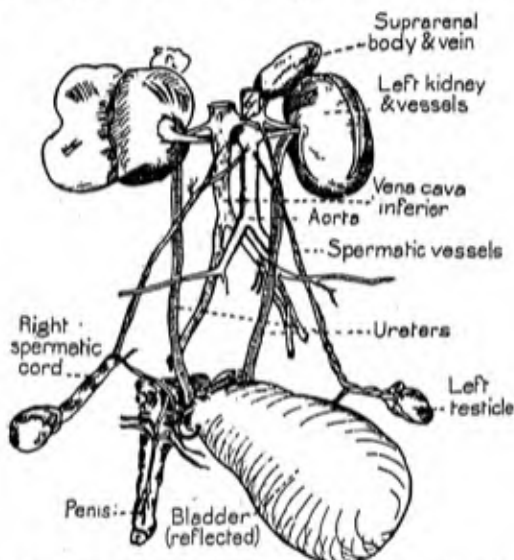


Fig. 1. Drawing of a dissection of the genito-urinary system of a Chimpanzee. From Tyson's "Orang-Outang, sive Homo Sylvestris. Or, the Anatomy of a Pygmie." London, 1699.

the subject were Linnaeus, Daubenton, Camper, Hunter, Soemmering and Blumenbach.

The *Systema Naturae* of Linnaeus (of which the first edition appeared in 1735) will remain for ever memorable to anthropologists from the fact that Man was therein restored¹ definitely to a place with other animals in a scheme of classification.

¹ Man was thus treated by Aristotle. In the time of Linnaeus, the various human races were described by Buffon in his *History of Quadrupeds* and their natural affinities were discussed. But Buffon disparaged all rigid classifications including that of Linnaeus.

Daubenton (1764), a colleague of Buffon, is to be credited with the first strictly scientific memoir in which the comparative anatomy of the skull was studied by means of angular measurements.

Camper's great work was first published in 1770. Born at Leyden in 1722, Camper had attained the age of sixty-seven when he died. But for the work of Tyson, that of Camper would hold the place of honour as anticipating the soundest and most productive methods of modern physical anthropology. Camper's researches dealt with the comparative anatomy of the Orang-utan (a chapter being devoted specially to its comparison with Man), with the

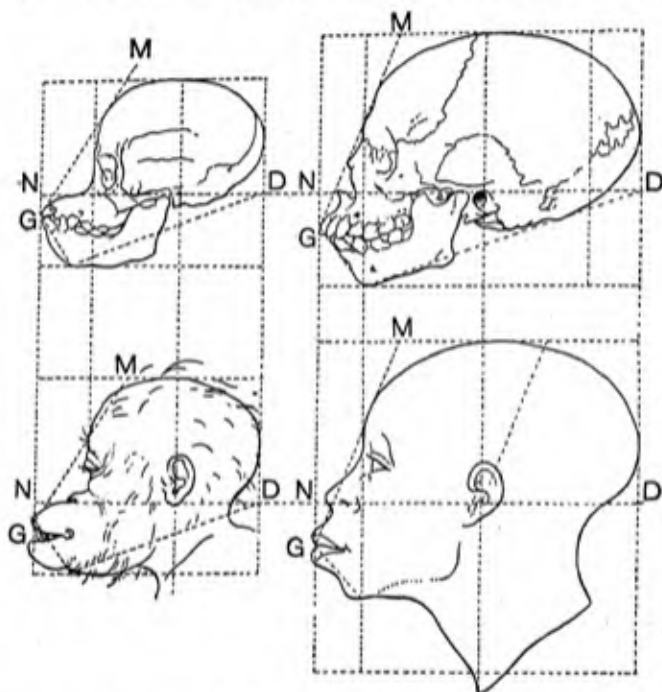


Fig. 2. Drawings of the head and skull of a young Orang-utan, and of a negro, to shew the method of determining the facial angle of Camper (cf. Chap. xi). From Camper's original memoir.

different varieties of anthropoid apes, with the organs of speech in the Orang-utan, with the significance and origin of pigmentation in the negro races, and finally with the comparative study of skulls. In this connection, special reference is due to the method employed, for it was based on the principle of projections, i.e. the comparison of forms and contours drawn in rectilinear projection. Errors due to perspective, such as occur when the object is viewed in the ordinary way, were thus eliminated. In the same treatise, Camper defines and explains the use of the facial angle (cf. Fig. 2)

which he devised, and through which his name will be perpetuated in the literature of craniometry.

The work of John Hunter (1728-1793) stands in a category apart from all others. If not avowedly anthropological, the researches carried out by Hunter in Comparative Anatomy define the field or extent of the larger part of modern Physical Anthropology. For the rest, it must be added that while in Hunter's work the anatomical notes are numbered in thousands, the physiological background is never lost to view. Herein, it is fair to believe, a clue will be found to Hunter's success. This vitalizing principle was rigidly maintained and may be studied to-day, not only in the literary monuments left by Hunter, but also in the noble Collection by which his memory is perpetuated.

The accomplished anatomist Soemmering published (in 1785) a monograph on the anatomy of a Negro, which has become classical. The author extended the comparative methods employed by Camper in the case of the external characters, to the details of every part and structure of the body. In this research again, we may notice the substitution of exact and precise information for speculative surmise. Not the least important point made by Soemmering was his observation that the brain-weight of his subject exceeded that of most Europeans. This very paradox (as it seemed even then to Soemmering) led him to anticipate (in part at least) important researches carried out a century later by Snell and Dubois. For Soemmering found that while the Negro's brain exceeded that of the European in weight, it held nevertheless a more lowly position when judged by a comparison of its size with the combined mass of the cerebral nerves. The absolute weight taken alone is thus deprived of value as an index of developmental status. It is further shewn that for the interpretation of the significance of the brain-weight, the size and complexity of the organs supplied by those nerves must be held accountable for a certain part (now called the "corporeal concomitant"). And finally, it is on the part which remains over, called by Soemmering the "superfluous quantity," that judgment as to the real "size" of the brain is to be passed.

Blumenbach is distinguished particularly by his studies in comparative human craniology (cf. Fig. 3). Born at Gotha in 1752, Blumenbach studied successively at Jena and at Göttingen, at which latter University he obtained a professorial chair: and at Göttingen Blumenbach died in 1840. Three characteristics seem to be prominent before all others in the character of this remarkable man. His extraordinary versatility in scientific pursuits has rarely been surpassed, even in the fatherland of Goethe, Helmholtz, and Virchow. Scarcely less impressive was his enormous range of literary acquaintance. A third point is that he was eminently a laboratory worker (sesshaft, as the Germans style it), for he travelled but little.

Blumenbach's principal contributions to science consist of a treatise on the "Natural Varieties of the Human Species" and of numerous craniological descriptions, to which must be added certain essays on the Natural History of Man, including an anatomical comparison of Man with other animals.

And the chief advances determined by these researches may be summarized as follows:

(1) The employment of the word "anthropology" as descriptive of morphological studies.

(2) Recognition of the fact that no sharp lines demarcate the several varieties of Mankind, the transition from type to type being imperceptible.

(3) The clear enunciation of a classificatory scheme of the varieties of Mankind, admittedly arbitrary, but devised with the object of facilitating study: the classification was based on considerations of the characters of the skin, the hair, and the skull.

(4) A clear enunciation of the influence of external causes in producing and perpetuating variations in animals, including Man; recognition of the origin of varieties through "degeneration"; Blumenbach thus very nearly anticipated some important discoveries reserved for Darwin at a later date.

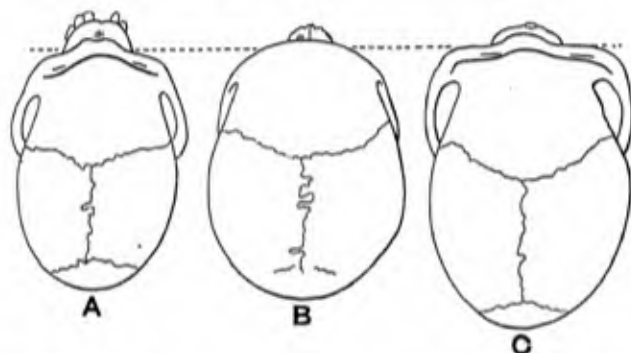


Fig. 3. Blumenbach's "norma verticalis" of three crania; A, an "Ethiopian"; B, a Georgian woman; C, a Tunguse. The different degrees to which the maxilla and the zygomatic arches project beyond the periphery of the cranial bones is to be noticed. (The figure is copied from that illustrating Blumenbach's *Works* as translated by the Anthropological Society.)

All differences in the cranial forms of Mankind were referred either to environment or to artificial interference. At the same time, it is suggested that artificial modifications may in time be inherited (cf. Blumenbach's *Works*, p. 121).

A general review of this work, together with that of the other authors cited, will shew that the main advances of the 18th century may be described as (a) the recognition of Man as a definite zoological form to which the methods and results of zoology are applicable, and (b) the replacement of general impressions by precise anatomical comparisons.

With the 19th century we are brought to further advances from the ground thus gained. The earlier half of the century is marked by at least one significant feature, viz.:—the foundation of societies for the scientific study of Man. The societies in question were founded in several countries, among which France and Great Britain took the lead. But the subject still remained in an undifferentiated condition, and a distinction between the studies of mental and physical attributes, or of nations and races, was not yet clearly marked. Such subdivision and specialization of study do not occur in the earlier phases of the life-history of a science, and Anthropology formed no exception to the general rule.

Anthropological Societies were founded, as has been mentioned, early in the 19th century, at an epoch when Hebraic cosmology was very generally and literally accepted. Against such literal acceptance protests were not lacking; the progress of zoological study (perhaps especially the results of observations on the geographical distribution of animal forms) had cast doubt on that part of the account relating to animals other than Man, just as the birth and growth of scientific geology had rendered necessary a revision of the opinion commonly held as to the history of the earth. These new creeds had not yet however gathered the force they were subsequently to acquire, and in particular the inferences drawn from them were not generally recognized as having an application to the special case of the origin of Man. None the less, certain French writers of the 18th century (Buffon, Cabanis¹, and Lamarck) had clearly suggested the possibility of the evolution of new species by the transformation of pre-existing forms of life, and had applied this reasoning to the case of Man in common with other animals. By so doing they kindled a spark of controversy which, after smouldering for half a century, was destined to break out as a veritable conflagration soon after the founding of the Societies of Anthropology to which reference has just been made. The labours of those Societies received thereby a stimulus the importance of which can hardly be over-estimated. But the point which it is here desired to emphasize is, that the early work of the Anthropological Societies consisted largely in the study of the outward appearance and cultural

¹ Cf. Hervé and Verneau in *L'Anthropologie*, 1905.

status of the various races of Man; when to these there is added the study of racial differences in human crania, an idea will be formed of the scope of their activity in the earlier decades of the 19th century. The problems of the origin of Man and of his relation to other animals still remained to be added. The revelation came in 1859.

Anthropology thus received a wider application than heretofore, and further, it is to be noticed that two men in particular (Darwin and Huxley) were instrumental in thus extending and rendering more precise the morphological aspect of this subject. The chief merits of Darwin in this connection may be summed up in the statement that he not only suggested the principle of Evolution as an explanation of the existence of the many varied animal forms, but brought it vividly before a very large section of the public; that he on the one hand indicated a possible explanation of the method of Evolution and on the other hand demonstrated that the reasoning involved is applicable to Man equally with other animal forms¹. This work was very appropriately supplemented by that of Huxley, who enunciated clearly the conclusions as to the relations of Man to other animals, which would be arrived at by the application of the line of argument laid down by Darwin. Huxley's lectures² given in 1863 are still the best introduction to this part of the subject (Fig. 4).

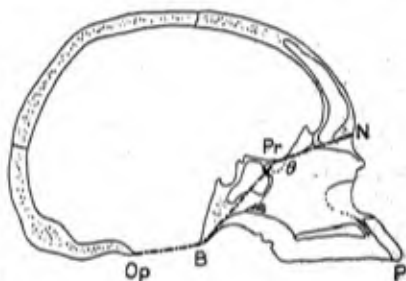


Fig. 4. The longitudinally-bisected skull of an aboriginal native of Australia, with the lines shewn by which Huxley's sphenothmoidal angle (θ) is included (viz. BPr , and NPr).

But the contributions of other investigators must not be overlooked entirely. The way had been prepared for Darwin and Huxley. Thus the "effects of environment" have been appreciated for centuries, perhaps from time immemorial. The opinions of Sir W. Raleigh in 1621 on this subject (cf. *Nature*, Jan. 23, 1902) are therefore to be regarded as "early" in a relative sense only. Their importance is due rather to the suggestion they

¹ Cf. Darwin, *On the Origin of Species* &c.: and *The Descent of Man*.

² "Man's Place in Nature." Similar lectures were given by Carl Vogt in Geneva.

afford of the stimulus given to biological studies by the discovery of the New World, and its peculiar fauna. Again the 17th century provides a reference (Vannini, 1616¹) to the idea of the descent of Man from monkeys, but it would be rash indeed to regard this as the earliest mention of that theory, the anatomical comparison of Man and the apes having formed the subject of controversy for at least a century before that time.

In the 18th century the stream of literary references increases to a flood. Here it is only possible to glance at a few of the more important developments. First we may notice the increased attention devoted to the principle of the gradation of characters. Thus we find in 1786² the bold statement of Hunter that the organ of hearing in fishes is "only a link in the chain of varieties displayed in the formation of this organ of sense in different animals, descending from the most perfect to the most imperfect in a regular progression." And in 1795 Charles White³ of Manchester applied the Hunterian method of comparison to Europeans and Negroes, as well as to different kinds of animals. Twenty years later, the genius of Hunter is reflected again in the admirable lectures of Lawrence on "The Natural History of Man."

These ideas on the gradation of characters are associated with speculations on the ancestry of Man in the remarkable work of Lord Monboddo⁴. Only two quotations can be given, but it will be agreed that it is truly startling to find such views clearly expressed in 1774, nearly a century before the publication of Darwin's great work. In discussing the origins of human society, Lord Monboddo writes (Book 2, chapter iii): "From the South Sea, I will come back again to Africa, a country of very great extent; in which, if it were well searched, I am persuaded that all the several types of human progression might be traced, and perhaps all the varieties of the species discovered." Finally, in closing a long exposition of the resemblances between Man and the apes, the author concludes (Book 2, chapter v): "That my facts and arguments are so convincing as to leave no doubt of the humanity of the Orang-utan, I will not take upon me to say: but this much I will venture to affirm, that I have said enough to make the philosopher consider it as problematical, and a subject deserving to be enquired into....."

We may notice that in 1794, Erasmus Darwin (grandfather of Charles Darwin) had inferred the quadrupedal attitude of human precursors, from observations on the position of the urethral orifice in the human bladder.

Such references must suffice to shew in what measure the ground had been cleared for the great workers of the 19th century. A word must now be added in reference to Dr Wallace, whose name will always be associated with

¹ Bendyshe, *Mem. Anth. Soc. London*, vol. i. 1863-4, p. 355.

² Hunter's *Works*, edited by J. F. Palmer, vol. iv. Preface, p. v.

³ *An account of the regular gradation in Man and in different animals and vegetables and from the former to the latter.*

⁴ *Origin and Progress of Language*. This invaluable memoir was brought to my notice by Dr Kohlbrugge. Cf. *Die morphologische Abstammung des Menschen*. Stuttgart, 1909.

the Darwinian theory. It is necessary to lay stress on the fact that Wallace was the first publicly to apply to Mankind the logical consequences of his own teaching and that of Darwin, as applied to forms of life in general. This particular application of general principles was made by Dr Wallace in 1864 (*Anth. Review and Journal*, vol. II. 1864; *Journal*, pp. clviii. *et seq.*), whereas the *Descent of Man* by Darwin, though in its inception actually earlier than the *Origin of Species*, did not appear till 1871. As may be surmised, Dr Wallace was immediately and vigorously attacked, even by anthropologists (such as the egregious Dr James Hunt). But it is impossible to enter here upon a detailed exposition of the controversies of that epoch.

The discovery of numerous precursors detracts little or nothing from the credit of Darwin, for to none had there been granted in such measure the talents of substituting experiment for speculation, of instantaneous perception of the significance of the results obtained, and unwearied industry in widening the basis of fact upon which arguments are to be founded.

Thus the attention of students was redirected to the investigation of the structure of the human body, in other words the study of Human Morphology. It is preferable in this connection to speak of Human Morphology rather than of Human Anatomy, for the former term implies the comparison of the architectural form of the human frame with those of other animals. Not that the study of Human Morphology was a newly-discovered field for activity; and it is here that the interest that attaches to Tyson's work becomes manifest; for the keynote of the treatise to which reference has been made is the morphological aspect of anthropology as studied by means of a detailed comparison. Moreover, as we have seen, Peter Camper of Amsterdam had supplemented Tyson's memoir on the Chimpanzee by a corresponding essay on the Orang-utan. In addition to this, the subversive theories of Lord Monboddo¹ were probably responsible for the appearance in 1779 of a communication from Camper on the vocal organs of the Orang-utan, compared with those of Man².

On the embryological side (a most important department of morphological study) Meckel, Tiedemann, and v. Baer (in the early part of the 19th century) had made discoveries of fundamental importance for the progress of the science.

New, however, was the widespread recognition, first that the study of the origin of Man now demanded the attention

¹ v. *supra*, p. 8.

² *Phil. Trans. Roy. Soc.* vol. LXIX.

and the interest of students of natural science, and secondly, that this problem, of which the solution had appeared so hopeless, might now be attacked by the same methods as were being applied with success to unravelling the origins of other members of the Animal Kingdom¹.

The range of anthropological studies was in this way very considerably enlarged about the middle of the 19th century and, in particular, the study of human crania (which has already been mentioned as forming a subsection of Anthropology from the time of Blumenbach) was now energetically pursued in various European countries. In this connection the names of Retzius, Huxley, Lucae, Virchow, Schaaffhausen, Flower and Turner² are of note, but above and beyond all these stands the French observer Paul Broca, whose work has had an almost incomparable influence on the study of Craniology³. This study has been spoken of as distinct from that of Human Morphology, but it is important to notice that the successful newcomers in this field recognized that Craniology is to be regarded as essentially a branch of Human Morphology, and that only in this way can it lead to reliable results: the omission to recognize this important fact has led to many misconceptions and to the vain expenditure of much misdirected energy in Craniology.

¹ The ancestry of the horse as demonstrated by Huxley is a good example in point.

² Professor Sir William Turner recently published a complete list of his works (published by Neill & Co., Edinburgh, 1910). Particular attention is directed to his Presidential Address to Section H, British Association for the Advancement of Science. Toronto, 1897.

³ Paul Broca was born in 1824. Educated as a surgeon, he not unnaturally first published work dealing with surgical topics, such as the surgery of aneurism. In 1859 Broca published a contribution to biological literature entitled "Hybridity," pointing out the interest of the phenomena of hybridity in connection with the stability and fixity of animal species. In this work the special case of man is discussed, and doubt cast on the occurrence of Eugenesis, or the fertility of the offspring of individuals of strongly contrasted race; these doubts have been resolved in the negative.

In the same year (1859) Broca published the first of a long series of works upon the prehistoric inhabitants of Western Europe; the first contribution dealt with the Ethnology of France, shewing the effects of invasions upon the primitive autochthones of that land. Numerous essays on the human skeleton and particularly upon the skull followed. Attention was then diverted to the soft tissues, and like Blumenbach, Broca worked out an anatomical comparison (*Parallèle*, as it is termed

In another direction, a memoir published in 1866 by Dr Langdon Down and entitled "Ethnic types in Idiots," marks an early stage in the study of Morphology in relation to Pathology. The names of Virchow and Metschnikoff stand out beyond all others in the history of this division of our subject, the importance of which can scarcely be exaggerated.

Some of its latest developments are discussed in an invaluable work recently (1911) published by Dr Hastings Gilford¹.

by French writers) of Man and the Apes. Recognizing the importance of the brain in the animal economy Broca devoted much time to its study. His contributions to the subject of Aphasia, and his recognition of the localization of the faculty of speech in the convolution which now bears his name (the inferior frontal convolution of the left cerebral hemisphere), are well known. And though his conclusions have not been altogether borne out in detail by the results of later workers, Broca's contributions to the morphology of the brain certainly place him among the foremost pioneers in that field.

Not the least of Broca's merits is his recognition of the necessity of accurate methods of comparison, and this led to his devising a multitude of delicate instruments of which the best known is perhaps the stereograph (cf. Fig. 5), a mechanical apparatus for tracing contours which can subsequently be superposed and accurately compared. Broca's extension of the use of "indices" in craniological studies, a method due to the elder Retzius and von Baer², is an important feature of his works, but is not a matter of such lasting or fundamental importance in regard to his scientific contributions as a whole.

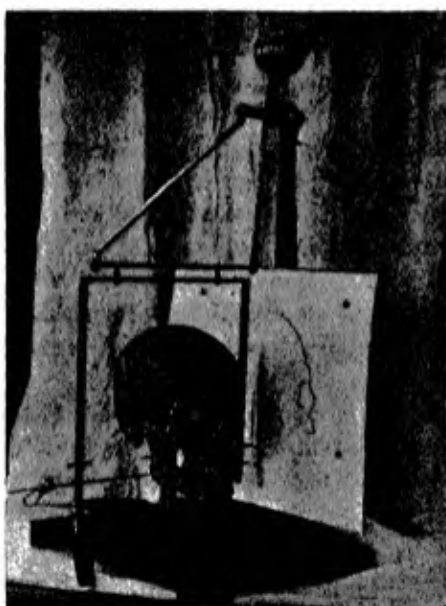


Fig. 5. The stereograph of Broca: a mechanical device for producing rectilinear projection drawings of crania or similar objects. For further description see Chapter x.

¹ *The disorders of post-natal growth.*

² v. Busk, *Nat. Hist. Review*, 1862, p. 357.

Apart from these extensions, the last two decades have witnessed the rise and progress of two entirely novel departments of research. For the biometric methods introduced by Galton and the principles involved in the Mendelian system are evidently applicable to the problems of human variation and heredity. And if it be admitted that the units employed in those researches are morphological in nature, it follows that the methods themselves are essentially aids to a more correct appreciation of human morphology.

But we meet with considerations of vast importance arising particularly out of the situation as viewed from the Mendelian point of view. It must suffice here to mention the conception of "unit-characters" and the mode of transmission of these. For in the light of the new teaching as expounded by such writers as Davenport, Cuénot and Blaringhem, the whole field is altered in regard to the rate of Evolution, and its mode of progress.

It is convenient to leave for a moment the various problems grouped under the general heading of Morphology and to turn to another aspect of the study of Man. For the advance effected through the fuller realization of the idea of Evolution in particular application to Mankind, necessarily influenced other considerations than such as are strictly morphological. In the light of Darwinian research it became necessary to investigate not merely the bodily structure of Man but also his intellectual powers and their manifestations: not only these, but even the origins of human society, and of arts and sciences of whatever kind, were gradually added to the list, so that Anthropological literature now deals with a variety of subjects so diverse as the studies of languages, of the special senses in civilized and savage races, of decorative art, of the origins of religion, of picture-writing, of children's games, of ceramics, of metallurgy, and of midwifery. In fact, Anthropology is no longer a single subject; it organizes a group of sciences, and consequently, to use the simile so ably put forward by Professor Tylor, it can well be compared to the frame used by mountaineers for the purpose of supporting a miscellaneous load. The convenience of the frame more than compensates for the slight additional weight imposed by it.

It is appropriate to remark in this connection that the theory of Evolution has proved to be of the utmost utility in the study,

not of Animal Morphology alone, but of all the above-mentioned subjects, widely different though they may at first sight appear to be. In every one of those subjects, without exception, may be found numerous instances in which the doctrine of Evolution has given the clue to the interpretation of a series of observations, and has afforded such a demonstration of otherwise unsuspected relations between them as no other known principle could have possibly furnished¹.

The foregoing notes may serve to give an idea of the protean nature of Anthropology; a subject which the individual will strive in vain to grasp fully in the course of his natural lifetime. It is therefore necessary to limit one's efforts to a certain region or section, and the section which will be the subject of consideration in the following chapters is that to which reference has been already made, viz. the morphological aspect of Anthropology; incidentally, however, it will be necessary to refer to slightly different branches of the subject.

The following aims may therefore be proposed as falling within the scope of this enquiry. In the first place, the attempt must be made to realize the position occupied by Man in the animal kingdom: and secondly, enquiry must be made into the nature of the ancestors of Man. Finally, we may be in a position to discuss the question whether the series of animal forms which has produced Man has now reached its termination or not.

In connection with the first two questions, the following main paths lie open. It must be repeated that the study of Morphology by means of Comparative Anatomy is the first step in such an enquiry.

The second line of enquiry is closely allied to the preceding, and consists in the study of Morphology by means of Embryology².

A third line of research is nearly connected with the other two; this is the study of Variations, both of outward appearance and inward structure. To this division, the study of Pathology in

¹ For examples consult Haddon, *The Evolution of Decorative Art*; Balfour, *Evolution in Art*.

² Related to this second line of enquiry is the study of the post-natal stages of development, in other words, the study of child-life and of children. In accordance with the general rule that the individual reproduces in his life-history the successive stages (or the principal ones at least) by which his species attained its position in nature, it is argued that the immature human individual should afford some suggestions as to the nature of the latter stages of human evolution.

its biological relations is clearly appropriate. And to the sum total of these subjects, the methods of Biometry and of Mendelian research will apply.

A fourth division consists in the study of Geographical distribution and its relation to Mankind. The influence of environment is so intimately connected with the factors of climate, that the vast importance of this question is clearly evident. Moreover it is to be noted that those factors are not entirely neutralized even by the resources of modern civilization, though their action may be somewhat affected thereby.

A fifth method, more closely allied to the first (that of Comparative Morphology) than to any other, involves the investigation of the characters of such fossil animals as may be supposed to have figured in the ancestral history of Man and his nearest allies among the animals still in existence. This section of the science of Palaeontology claims much attention in the attempts to solve the problems of our subject.

Having discussed the general position of Man in Nature, it will be necessary to consider the various human races, and to enquire whether some of those races are to be regarded as morphologically inferior to others, and especially whether the races which are commonly accounted as lower in the scale of civilization and culture are also inferior in morphological status. Should this be established, it will next be necessary to ascertain whether such morphologically inferior forms can be considered as representatives of the generalized human ancestors. We thus enter on a division of the second great question, viz. that of the appearance and nature of the ancestral animal-forms which led up to Man.

The foregoing notes will give an idea of Human Morphology as studied from the standpoint of Anthropology; the immediate subject of consideration is thus seen to be the place of Man in the zoological series, or animal kingdom. Without entering into an elaborate exposition of various types of life, it will suffice to say that judged by his structure Man is undoubtedly a vertebrate animal of the class Mammalia. Starting from this point, it is proposed to briefly study the characteristics of Mammals so as to understand how it is that this statement as regards Man can be justified. The following chapter will accordingly deal with Mammalia in general.

SECTION A

COMPARATIVE ANATOMY AND MORPHOLOGY OF EUTHERIAN MAMMALS

CHAPTER II

THE MAMMALIA: AND THE APPLICATION OF THE METHODS OF MORPHOLOGY TO THEIR CLASSIFICATION

It is necessary at the outset to give a brief description of the animal forms with which we are chiefly concerned, and to treat of them in a methodical manner.

Man's nearest relations are members of a class of vertebrate animals called Mammalia. Of this class three sub-classes are recognized, and it must be noted that the members of two of these three sub-classes are comparatively few in number and not natives of Europe; an example of one of these sub-classes is the Australian spiny ant-eater, and the kangaroo is an example of the other. The third sub-class contains a larger number of animal forms, and to it belong all our indigenous mammals.

One can imagine several ways in which the various mammals might be grouped for purposes of description: for instance, they might be arranged according to their geographical distribution, or else according to the nature of their food, or again according to their habits: and the first-mentioned means of distinction might be called a climatic criterion, which would for instance distinguish arctic animals from those living in tropical latitudes,

while the second means of distinction (diet) would be called a physiological criterion. Thus it is that we are compelled at the outset to state clearly the basis upon which we proceed in a classification. In the present case the basis is Morphology, and our criterion is the criterion of structure. In this classification, animals will be considered as more or less closely related, according as their structure is more or less similar in its details. It is necessary to enter into details for two reasons. First, because the very fact of the name "vertebrate" being applicable to all the animals about to be considered, implies that they possess one general morphological character in common, and indeed that they are constructed upon a similar plan. Clearly, therefore, we must know more than this elementary fact before proceeding to any kind of arrangement by groups. But in the second place we have to remember that the principle of basing relationship on the ground of similarity in structure is of fundamental importance. That the principle itself may be overthrown one day is conceivable.

That contingency is still sufficiently remote to leave an ample margin of confidence in our guide, provided always that conclusions are based on evidence drawn from a number of details and not from single individual features or characters. This note of warning must needs be sounded in view of the cases adduced as examples of "Convergent Evolution." Without close attention to details, the observer may well be deceived in such instances. Sometimes, as for example where the fish is compared with the whale, the investigation need not proceed far before the real differences are exposed. But again, when the marsupial mole (*Notoryctes*) and the European mole are compared, a finer analysis is required.

The problems encountered in Physical Anthropology involve greater difficulties and a corresponding increase in the attention due to details. And in the more particular consideration of the principles of Morphology, the following point is of interest and importance. It will be remembered that the vertebrate body is composed of a number of very different parts, and that although these are demonstrably similar to one another, inasmuch as they all possess cellular structure, yet the cells have undergone specialization in several different directions, with the consequent production of a number of tissues from which have

been built up systems familiar to us as the skeletal system, digestive system, and so on. It is indeed an important consideration in Vertebrate Morphology, that specialization of primitively similar cells occurs, resulting in the production of tissues and systems. From the general consideration of the vertebrate body it is however necessary to pass to that of the several tissues and systems.

In the study of the morphology of the various systems we find that each is constructed on a certain plan, so that each may be referred to a fundamental, primitive, or type-form. Thus the primitive forms of the central nervous system, or of the skeletal or arterial systems, are common expressions. Each system of a given animal reveals a more or less altered representation of that primitive form. The point before us consists in the fact that in such a given instance (and this is especially true of Mammals), though each system will be found to represent a modified form of the primitive type, yet the amount of modification undergone is different for each system. Thus an animal may possess a nervous system of very primitive, *i.e.* slightly modified, form together with an extremely modified integumentary system. It follows therefore that in assigning a place in the classification to a given animal, attention must be paid to the morphology of each and every system, and a position must only be assigned to it after a final summary of all the evidence has been made. Thus an animal like the hedgehog presents us with the morphological combination of a brain of simple conformation, together with an integument of very modified character. Taking other morphological points in the anatomy of the hedgehog, the general balance of the summing up of evidence indicates that on the whole this is a little modified, *i.e.* a comparatively simply-constructed animal, which is the result one would have arrived at from the study of the brain alone, though opposed to the indication that would be afforded if the observation had been confined to the integument.

The disadvantage attendant on the employment of a single criterion, such as the conformation of a single organ or system, may be further illustrated by the example of the genitalia in Man. Judged by the single characteristic of the morphology

of the genital organs, Man differs more widely from Woman than from an individual of his own sex in such a comparatively lowly form as a shrew-mouse. It follows therefore that inferences from observations on various systems and organs must be introduced into what may be called the morphological balance sheet, due allowance being made for conditions determined by sex and by age.

The foregoing remarks will serve to indicate the importance of taking into consideration the evidence given by several systems and of summing up the results thus obtained.

In so doing, attention is directed to the relative value of the different pieces of evidence. To illustrate this side of the question, the simple example already adduced, of the Fish and the Whale, may be employed again. Thus in this instance, the evidence of the respiratory organs admittedly overrides that provided by the external form and proportions. Such ratings or assessments are to some extent matters of convention and agreement. Organs which are less exposed to external influences are held usually to be the surest guides. But while it is generally safe to rely more implicitly on the form of the brain or heart, for instance, than on the external characters, yet each case must be decided upon considerations peculiar to its circumstances. These again bring in physiological principles which cannot be divorced from those of Morphology.

We may now note, although this is an anticipation, that when the criterion of structure is employed, the determination of the position and relations of Man in the Class Mammalia is more easy than when other criteria are made use of. On this subject the verdict of Morphology is clear and unhesitating.

It is further to be noted that the most primitive morphological type of mammal is as a rule, though not always, the most simple; and the less primitive is often, though by no means always, the more complex in construction.

The comparative method of study is applicable to all the mammalian forms, and when the test of Morphology is applied to Man himself it will be found as has been said that his relative position is well defined. This application of the principles of Morphology to the special case of Man constitutes the essence of Physical Anthropology.

In returning to the subject of the Classification of Mammals¹, we must then first consider the combination of morphological characters which entitle the animal possessing them to be ranked as a mammal. In view of what has just been noted as regards the different systems, it will not be a matter of surprise that the characters selected are taken from several, and not all from any one system.

*The Distinctive Characters, and the Classification of Mammals*².

The Mammalia are air-breathing vertebrates, with warm blood, and with an epidermal covering in the form of hairs.

I. The bodies of the **vertebrae** are in nearly all mammals ossified each from three independent centres, one of which develops into the centrum proper, while the others give rise to two discs of bone—the epiphyses. Also characteristic of the spinal column of mammals are the discs of fibro-cartilage, termed intervertebral discs, which intervene between successive centra.

II. The **skull** has two condyles for connection with the atlas, instead of the single condyle of the Sauropsida (Birds and Reptiles); and the lower jaw articulates with the skull in the squamosal region without the intermediation of the separate quadrate element always present in that position in Birds and Reptiles³.

¹ Notice that the character, viz. the nutrition of the young by the secretion of milk-glands, which has given the Class its name, is not a primarily morphological, but a physiological feature. Its morphological counterpart is found in the mammary glands themselves. The first employment of the term "Mammalia" is ascribed by Gill and Gregory to Linnaeus.

² Owing to the courtesy of authors and publishers, the classification of the Mammalia as given by Messrs Parker and Haswell in their *Textbook of Zoology*, Vol. II. (Macmillan), is here available; though it has been followed generally, some modifications necessitated by the advance of knowledge have been made.

³ Spurrell (*P. Z. S.* 1906, II. p. 7) points out an interesting feature related to the possession of a large quadrate bone. It is submitted that in one type of mouth, the articulation of the mandible is in the plane in which the teeth meet. This type occurs even among the Mammalia, e.g. the Carnivora. Lateral movements are negligible in this type. In the second type, the articulation is not in the same plane as that in which the teeth meet. In Reptiles it is below that plane, and the displacement is due to the length of the quadrate bone. In Mammals the plane of teeth is displaced downwards and this is due to the development of a distinct "ascending ramus" of the lower jaw. In the second type, all the teeth may meet simultaneously, and in many Mammals, lateral movements are possible.

III. Each of the long bones of the limbs (in the young condition) is composed of a central part or shaft, and of terminal epiphyses, the latter only becoming completely united with the shaft at an advanced stage.

IV. The ilio-sacral connection is pre-acetabular: there is a cruro-tarsal joint.

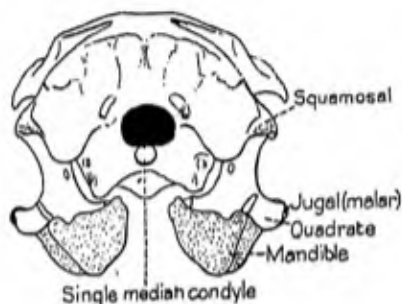


Fig. 6.

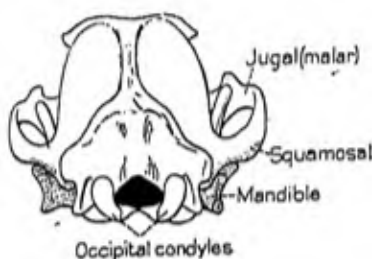


Fig. 7.

Fig. 6. Occipital view of the cranium of a Bird (*Larus*); to show the single median occipital condyle, and the intervention of the quadrate bone between the mandible and the cranial wall.

Fig. 7. Occipital view of the cranium of a Dog; to show the twin occipital condyles, and the direct articulation of the mandible with the cranial wall, without the intervention of a quadrate bone.

V. In the Mammalian pectoral girdle, the coracoid of Birds and Reptiles is usually represented only by a vestige or vestiges which unite with the scapula in the adult. [Figs. 8, 9, and 10.]

VI. Mammals are typically diphyodont, *i.e.* have two sets of teeth—a milk or deciduous set, and a permanent set: some are monophyodont, *i.e.* have only one set. The teeth are thecodont, *i.e.* the base of each tooth is embedded in a distinct socket or alveolus in the substance of the bone of the jaw: and nearly always the teeth in different parts of the jaw are clearly distinguishable by differences of shape into incisors, canines, and grinding teeth, *i.e.* are heterodont; in some instances the teeth are all alike (homodont).

VII. A cloaca is absent, except in the Prototheria.

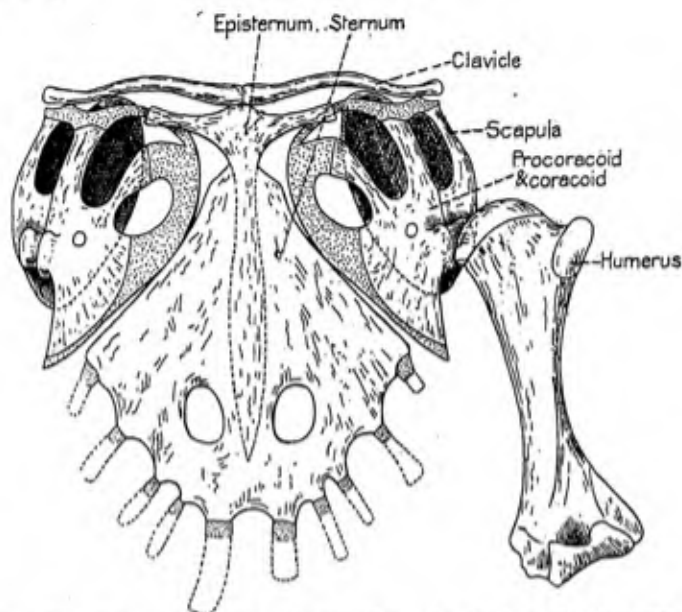


Fig. 8. Shoulder girdle of a Reptile (*Iguana*); to show the elements of the girdle in a comparatively undifferentiated condition.

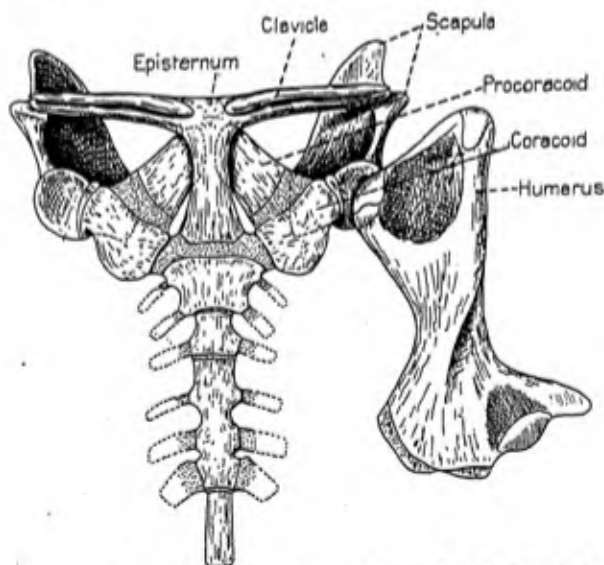


Fig. 9. Shoulder girdle of a Prototherian Mammal (*Echidna*); to be compared with Fig. 8. Several of the primitive constituent elements of the girdle are still distinct.

VIII. A movable plate of cartilage—the **epiglottis**—represented only by a rudiment in some Amphibia and Sauropsida—overhangs the slit—commonly called **glottis**—leading from the pharynx into the cavity of the larynx.

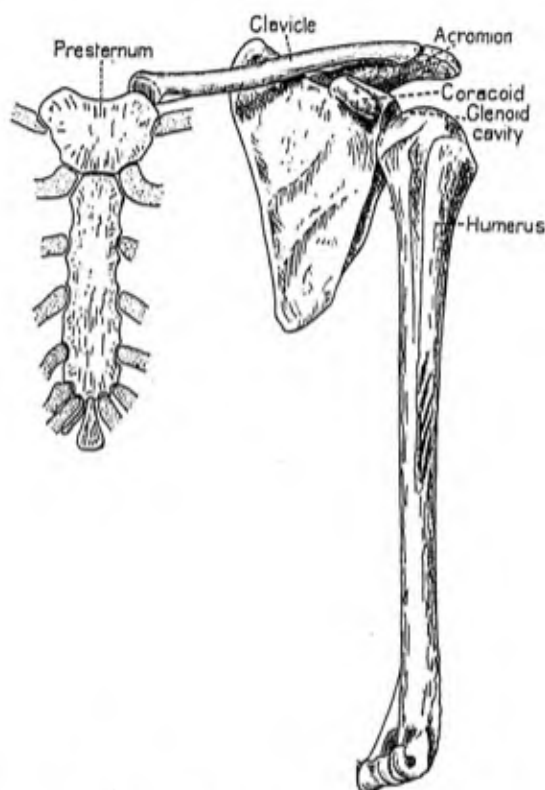


Fig. 10. Shoulder girdle of an Eutherian Mammal (Man); to shew the reduction in number of elements remaining distinct.

IX. A partition of muscular fibres, usually with a tendinous centre—the **diaphragm**—divides the cavity of the body into two parts, an anterior—the **thorax**—containing the heart and lungs, and a posterior—the **abdomen**—containing the greater part of the alimentary canal with its associated glands—the **liver** and **pancreas**—and the **renal** and **reproductive organs**.

X. The **lungs** are freely suspended within the cavity of the thorax.

XI. The **heart** is completely divided into two halves—a right and a left—between which there is no aperture of communication. Each half consists of an auricle and a ventricle, opening into one another by a wide aperture, guarded by a valve composed of three membranous cusps on the right side, two on the left. The right ventricle gives off the pulmonary artery: the left gives off the single aortic arch, which passes over to the left side, turning round the left bronchus in order to run backwards as the dorsal aorta: it therefore represents the left aortic arch of Reptiles.

XII. The **blood** is warm. The red blood corpuscles are non-nucleated and usually circular.

XIII. The two **cerebral hemispheres**, in all but the Prototheria and Metatheria, are connected together by a band of transverse fibres—the corpus callosum—not represented in the lower vertebrates. The dorsal part of the mid-brain is marked by four eminences—the corpora quadrigemina. On the ventral side of the hind brain is a transverse band of fibres—the pons varolii—by which the lateral parts of the cerebellum are connected together.

XIV. The **ureters** (except in the Prototheria) open into the bladder. Mammals are all, with the exception of the Monotremes, viviparous.

XV. The **foetus** (except in the Prototheria) is nourished before birth from the blood-system of the parent through a special development of the foetal membranes and the lining membrane of the uterus, termed the placenta. After birth the young mammal is nourished for a longer or shorter time by the milk or secretion of the mammary glands of the parent.

Such are the characteristics common to all mammals. The animals presenting these characters have been classified as follows.

CLASSIFICATION (Parker and Haswell):

CLASS MAMMALIA.

Sub-Class 1. Prototheria.

Order Monotremata.

Sub-Class 2. Theria.

SECTION A. *Metatheria*.

Order 1. Polyprotodontia.

Order 2. Diprotodontia.

SECTION B. *Eutheria*.

Order 1. Edentata.

Order 2. Cetacea.

Order 3. Sirenia.

Order 4. Ungulata.

Order 5. Carnivora.

Order 6. Rodentia.

Order 7. Insectivora.

Order 8. Cheiroptera.

Order 9. Primates.

While the system of classification thus set forth may be retained on account of its simplicity, the results of recent work shew that in several respects, it fails to represent correctly the relations indicated by the actual structure of the animals concerned. Speaking generally, all the amended classifications are more complicated. In some of them the attempt is made to arrange the several Orders of the Eutheria in groups, though only so far as is warranted by the facts. The scheme (Fig. 11) published by Gregory (1910) is relevant, since it exhibits relationships based upon discoveries of extinct mammals. Through these extinct forms, some existing Orders become associated. Other living Orders (*e.g.* Ungulata) are shewn to include subdivisions (Artiodactyla and Perissodactyla) of diverse origin.

INFRA-CLASS EUTHERIA.

	<i>Super-orders</i>	<i>Orders</i>	<i>Sub-orders</i>
(a)	Therictioidea	Insectivora Carnivora	Lipotyphla
(b)	Archonta	Menotyphla Dermoptera Cheiroptera Primates	Prosimiao Anthropoidea
(c)	Rodentia	Glires	
(d)	Edentata	? Tubulidentata Pholidota Xenarthra	
(e)	Paraxonia	Artiodactyla	
(f)	Ungulata	Mesaxonia	Perissodactyla
(g)	Cetacea	Odontoceti Mystacocoti	

It will suffice to remark here that (i) the term Infra-class is substituted for the word Section employed by Parker and Haswell, (ii) the two Orders of marsupial animals are now accorded sub-ordinal rank only, and (iii) the Orders of Eutheria have been increased to fourteen in number.

Without entering into a detailed description of the characters of the several Orders, it will suffice to enumerate those of the Sub-Classes and of the Sections.

SUB-CLASS I. PROTOTHERIA.

1. The vertebral centra lack epiphyses, or these are only imperfectly developed.

2. The bones of the skull coalesce early, by the obliteration of the sutures (the skull thus resembling that of birds).

3. A large coracoid, articulating with the sternum, is present.
The pro-coracoid is distinct. Fig. 12.

4. A T-shaped episternum is present.

5. Two epi-pubic bones are present.

6. A cloaca is present, into which the ureters and urinary bladder open separately.

7. The corpus callosum is not developed in the brain.

8. The oviducts are distinct throughout.

9. The mammary glands are devoid of teats.

10. The ova are meroblastic, and are discharged in an early stage of their development, enclosed in a tough shell.

This Sub-class comprises a single living Order, the Monotremata, including the Duck-bill or Platypus (*Ornithorhynchus*), and the Spiny Anteater (*Echidna*). Many features suggest reptilian relationship and ancestry, while other characters are adaptative. Reptilian resemblances are harder to recognize in the Theria, which have acquired new features.

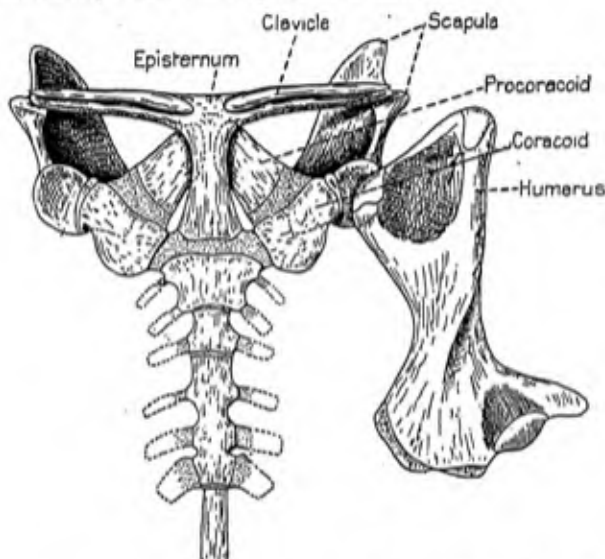


Fig. 12. Shoulder girdle of a Prototherian Mammal (*Echidna*); to be compared with Fig. 8. Several of the primitive constituent elements of the girdle are still distinct.

SUB-CLASS II. THERIA.

1. The vertebral centra possess distinct epiphyses.
2. The skull bones do not in most cases completely coalesce, most of the sutures remaining distinguishable throughout life.
3. The coracoid is vestigial [as is also the pro-coracoid] (Fig. 10).
4. The episternum is incorporated in the substance of the presternum (Götte).

5. The cloaca is not present (Gadow restricts this statement to males).
6. The oviducts are united in a longer or shorter part of their course.
7. The mammary glands are provided with teats.
8. The ova (except in some members of Section A of the Theria) are holoblastic, and the early development of the young takes place in the uterus.
9. The epi-pubic bones and the corpus callosum are variable in their occurrence.

SUB-CLASS THERIA. SECTION A. METATHERIA OR
MARSUPIALIA.

1. Theria, in which the young are born in a comparatively undeveloped state, and are sheltered during their later development in an integumentary pouch, the marsupium.

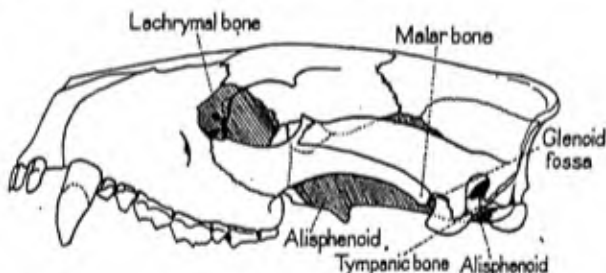


Fig. 13¹. Cranium of *Sarcophilus*, a Metatherian or Marsupial Mammal; the shaded area denotes the extent of the alisphenoid bone along the cranial wall; note the extent backwards of the malar bone, and the extent forwards of the lachrymal bone. Cf. Fig. 14.

2. In the skull (Fig. 13), the tympanic cavity is partly bounded by the alisphenoid; the jugal (malar) bone furnishes a contribution to the floor of the glenoid cavity.

¹ In Figs. 13 and 14, a good example of "convergence" in evolution may be remarked. The convergence is perhaps most definite in respect of the dentition; the latter is adapted to a carnivorous diet in both instances. In the two figures, stress is laid on the osteological details serving to differentiate the two skulls, which are seen to be only superficially alike.

3. Epi-pubic bones are present and well developed.
4. A single sphincter muscle surrounds both anus and urogenital aperture.
5. The corpus callosum is absent.
6. The placenta, when present, is functional for only a short period.

The Metatheria (or Marsupialia) are divisible into two Orders, distinguished principally by the characters of their dentition, particularly of the incisor teeth. There is thus to be distinguished the Order Polyprotodontia, whose members have numerous incisor teeth (more than three on each side). The Opossums belong to this Order. The second Order (Diprotodontia) possess not more and usually fewer than three incisor teeth on each side. The Kangaroos are examples of this Order. The Metatheria bridge the gap between the Prototheria and the Eutheria. The latter may be held to share an ancestor with the Metatheria, and this ancestor in turn was derived probably from a Prototherian form.

SECTION B. EUTHERIA.

1. Theria having no marsupium. The young are nourished *in utero* for a considerable period, through the agency of a placenta.

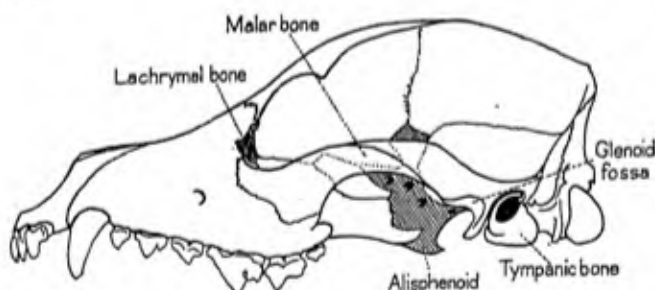


Fig. 14. Cranium of an Eutherian Mammal (Dog): for comparison with Fig. 13; note the smaller extent (backwards) of the alisphenoid (shaded), the malar and lachrymal bones.

2. In the skull (Fig. 14), the alisphenoid does not contribute to the wall of the tympanic cavity; nor does the jugal (malar) (except in Hyracoidea and some Rodentia) contribute to the floor of the glenoid cavity.
3. No epi-pubic bones are present.

4. The anus and urogenital apertures are not surrounded by a common sphincter.

5. A corpus callosum is present.

Referring, as before, to the most recent classification, we find, in the work of Gregory, the following scheme of "diagnoses," which provide additional osteological data.

Sub-class Prototheria.

Reptilian angular bone absent (at least in *propria forma*).

Oviparous: no secondary teeth. Shoulder-girdle (Fig. 12) and humerus much as in the mammal-like reptiles: prespinous fossa of the scapula absent or rudimentary, lower part of the anterior border of the scapula corresponding to the spina scapulae and acromion of higher mammals; large coracoids and procoracoids overlapping in the mid-ventral line; large T-shaped interclavicle; glenoid facet for humerus very near the sternum. Epi-pubic bones present. No corpus callosum.

Habits: primarily semi-fossorial.

Sub-class Theria.

Viviparous, with teeth. Prespinous fossa present (much reduced in Cetacea); coracoid (Fig. 10) and pro-coracoid reduced, not touching sternum; interclavicle absent or vestigial; glenoid facet for humerus widely separated from sternum.

Habits: primarily semi-arboreal.

I. Infra-class Metatheria.

Epi-pubic bones. No corpus callosum. Angle of mandible inflected (save in *Tarsipes*); typically with only the posterior milk molar tooth replaced by a successor; $p \frac{2}{3}$ absent; molars typically $\frac{1}{2}$.

II. Infra-class Eutheria.

No epi-pubic bones. Corpus callosum present. Angle of mandible typically not inflected; all the antemolar teeth typically represented by both milk and permanent teeth; $p \frac{2}{3}$ typically present; molars typically $\frac{3}{4}$.

The Eutheria can be divided into at least nine Orders distinguished by the various combinations of morphological characters enumerated in the following scheme.

Order 1. Eutheria, in which the teeth are absent in the adult or are imperfect; the sacral vertebrae are frequently in excess of the number usual in other orders. The coracoid process is usually relatively larger than in other Eutheria, and does not become completely fused with the scapula. The organisation of the brain is very variable. Edentata.

Order 2. Aquatic Eutheria with large head, fish-like body devoid of hairy covering, the pectoral limb paddle-like, the pelvic limbs absent, and with a horizontal caudal fin. The clavicles (collar bones) are absent, and the pelvis is vestigial. Teeth may be absent and replaced by sheets of baleen (or whalebone). The conformation of the nostrils and of the larynx is peculiar. Cetacea.

Order 3. Aquatic Eutheria with moderate-sized head, with porpoise-like body covered with a scattered covering of hairs: the pectoral limbs are paddle-like, the pelvic limbs absent. The clavicles are absent and the pelvis is vestigial. Teeth are present, and the palate bears rugose horny plates. The larynx is not modified as in the Cetacea. Sirenia.

Order 4. Terrestrial, chiefly herbivorous Eutheria, with hairy covering abundant or scanty; the terminal phalanges of the digits, upon which the weight of the body usually falls, nearly always invested with solid horny hoofs. The clavicle is absent. The teeth are heterodont and diphyodont; the scaphoid and lunar bones of the carpus (wrist) are always distinct. The digits are often reduced in number. Ungulata.

Order 5. Eutheria, chiefly carnivorous, with furry integument: digits in manus and pes never less than four, and all provided with claws more or less retractile. The clavicle is variable in its presence, but it is never complete. The teeth are heterodont and diphyodont. The scaphoid and lunar elements of the carpus (wrist) are always united; the brain usually highly developed. Carnivora.

Order 6. Vegetable-feeding Eutheria, mostly small in bulk, with furry or spiny integument, clawed digits and usually plantigrade limbs. The dentition is heterodont and diphyodont, and the form of the incisors is chisel-like: these teeth grow from persistent pulps. Rodentia.

Order 7. Insectivorous Eutheria with nose usually prolonged into a short soft muzzle; with furry or spiny integument, clawed digits, and usually pentadactyle plantigrade limbs. Clavicles are present. The dentition is heterodont and diphyodont, and the

molars have pointed cusps: incisors are never fewer than two in the lower jaw on each side. The brain is very simple in conformation. Insectivora.

Order 8. Eutheria in which the pectoral limbs are modified to form wings, the bones being greatly elongated so as to support a broad web of skin extending to the hind limbs posteriorly. The ulna is vestigial, the clavicles well developed. Cheiroptera.

Order 9. Eutheria with prehensile limbs (adapted to arboreal life), the thumb and great toe being more or less completely opposable to the other digits. The digits are nearly always five in number, and are provided usually with flat nails: the clavicles are well developed. The brain is variable, but may present high conditions of development of the cerebral hemispheres. Primates.

It is to be remarked that although numbered from 1 to 9, it does not follow that this arrangement places the various Eutherian Orders in sequence according to the morphological status, a subject to be discussed in the next chapter. Here it is to be said that the Edentata, Ungulata, and Insectivora as defined above are the Orders most distinctly open to criticism. In other words, each of these three Orders includes within its own limits animals which can be admitted only on the plea that simplification is a prime necessity for the purposes of study. We have just seen (p. 26) that the most recent classification provides fourteen Orders instead of the nine given above. And there is much evidence to support such an increase. Yet the older system is found to be generally useful, and it is applicable to a large number of mammals; its retention is justified on these grounds as well as on account of its simplicity. That it is after all largely conventional, although based on the observed facts of animal structure, cannot be too strongly urged; but the advantage conferred by the mere fact that we can classify mammals is great, for it enables us to compare their forms and characters much more easily than if they were not susceptible to reduction to such order. But like conventional systems of other kinds, it has its limits; in other words, it does not apply to every animal. For there are animals which, when examined in the light of morphology, prove hard to fit into this classification. When we meet with such an instance, we should therefore remember

that it does not prove that the classification is bad or deceptive, but it shews rather that animals have been evolved without regard to any such conventional system of classification.

Here we find for consideration two points of view; of these we may take first the older: this, though it needs much qualification, is far from being entirely erroneous.

A. *Series continuous: intermediate forms "ancestral."* On the hypothesis that the method of the origin of species is an evolution, it follows quite naturally that animal forms should merge into one another by small gradations, and that classification, or grouping in classes, is actually only possible in view of the fact that large numbers of animal forms have failed to maintain their places in the struggle for existence. Had they not failed, it would be possible to collect a demonstration-series of animal forms ranging from the Amoeba to Man without any break or interruption. To-day the series is discontinuous and incomplete, and the systematist seizes on isolated groups, giving each a special name in his classification. And what of the animals between these groups? Some, having failed in the struggle for existence, can only be directly known to us by such of their parts as have been preserved in a fossil form. The skeletal parts only are as a rule thus preserved, and incidentally this shews the importance of osteology in morphological study. Such are the animal "links" which have been referred to as "missing." A few intermediate forms have persisted down to our time, and these animals prove hard to fit into a rigid system of classification.

B. *Series discontinuous: intermediate forms not necessarily ancestral.* Another view results from the cogency of two important objections brought against that just explained (A). These objections have been stated so perfectly by Galton (*Natural Inheritance*, p. 32) that here only a few words will be added in order to indicate their nature. In 1889, we find Galton objecting to the assumption that the gradations must necessarily be small or imperceptible. He laid stress on the clear and abundant evidence "not only of the appearance of considerable sports, but of their remarkable stability in hereditary transmission." And to-day, the expressions "discontinuous variation," and "mutation" (indicative of wide gaps between the successive forms and of differences in regard to their stability in descent), are continually recurrent.

Not only is the ground thus cut away from the claim that gradations are small in every case, but a far more important sequel follows. To explain the origin of small variations has seemed easier than to account for the wider "sports"; and for this some reason exists, since in the "smaller" cases, an appeal can be made to comparatively familiar (if not intelligible) factors of environment, such as climate or nutrition and their variations. These seem inadequate to account for "sports," and until a natural basis explanatory of the appearance of the latter is provided, no demonstration of "descent by evolution" can be considered flawless.

The first objection thus reminds us that evolution proceeds at a variable

rate; also it is claimed that evolution is discontinuous; again the urgency for an extended study of the characters called determinants (Cuénot) is clearly indicated.

The second objection is scarcely less important, and it relates to the interpretation placed upon intermediate forms. The usefulness of these examples in suggesting and explaining the general trend of evolution is unquestioned. They fill what otherwise would be gaps, and they reduce the extent of gradations. But it is clear from the first objection that intermediate forms need not constitute the actual line of descent; it is certain that many of them are not "ancestral," and a warning must be given against the common tendency to regard them in that light. But even those to which the term "ancestral" may not be applied, existed or do exist, and their position and relations demand elucidation. This is a very serious matter. For it is by some alleged (cf. Galton, *op. cit.* p. 33) that at least in certain instances, intermediate forms are to be regarded as "unstable varieties, whose descendants had reverted: they might be looked upon as tentative and faltering steps, taken along parallel courses of evolution, and afterwards retraced." If we add that the descendants might have also died out, and that some of the parallel courses of evolution had come to an end, then the foregoing proposition need only to be stated to compel acceptance. Evidently the difficulty remains that many intermediate forms of the highest interest are represented by only the most scanty fragments. To determine from these whether their possessor was in the ancestral line, or alternatively on a side-track, has provided matter for many an animated discussion, yet the difficulty is too often ignored. Its solution or removal is of fundamental importance in regard to such instances as the fossil remains from Trinil (*Pithecanthropus*), Mauer (*H. heidelbergensis*), and Piltdown (*Eoanthropus*). Returning to the general question of Evolution, it may be repeated that, even with such qualifications, the general analogy of a sequence or chain is still perfectly justifiable.

It should be further remembered that though in an uniform linear chain all the links are of equal value, yet in the variable series of animals known to us, we may chance to find isolated links of very different significance, the difference depending on the groups of animals connected by the link, whether the latter be known in the fossil or recent state. Moreover the metaphor of a linear chain is not so exact as that of a sheet of chain-armour in which a single link may bring three or four other links into mutual relation.

To take some examples, there may be cited such animals as the *Archaeopteryx*, a form which suggests a link between the *Class* of Birds and the *Class* Reptilia: the *Galeopithecus volans*,

which occupies an analogous position, but merely with regard to *Orders* (viz. the Insectivora, Cheiroptera and Primates) of the Class Mammalia: the *Cynopithecus* monkey of Celebes, which connects the *Genus* *Macacus* with the *Genus* *Cynocephalus*, within the limits of the Order Primates. Inasmuch, however, as we are dealing here principally with animals of the Class Mammalia, it follows that the links with which we are concerned will be comparable in point of importance with the two latter examples, rather than with the first-mentioned instance.

We have seen that the cases of such intermediate forms offers excellent opportunities of employing and testing the principles of morphological examination upon which is based the system of classification here set forth.

CHAPTER III

THE MEMBERS OF THE MAMMALIAN ORDER PRIMATES

IN the foregoing chapter the relative positions of the various Orders of the Class Mammalia were briefly reviewed from the standpoint of evolution. If it be assumed that the typical or representative mammal has during the period of its evolution passed through vertebrate stages corresponding respectively to those of the Fish, Amphibian, and Reptile, it seems intelligible that in some mammals a greater number of ancestral characters occur than in others. Such mammals as possess a greater number of such reminiscent characters should be regarded as primitive, while others should be described as less primitive, or more highly evolved.

From this standpoint there is much evidence for assigning the lowest place among the Mammalia to the Order Monotremata composing the Sub-class Prototheria. In series above these, and consequently less primitive in their degree of evolution, are the Metatheria, among which the Order Polyprotodontia is more primitive than the Diprotodontia. Above the Metatheria¹ come the Eutheria, consisting as has been already remarked of some nine Orders.

Allusion has been made already (p. 32) to the difficulties met with in grouping the various Eutherian Orders. The accompanying

¹ It is not surprising to find that while the Prototheria and Metatheria may thus be regarded as primitive or slightly evolved, there are not lacking those who would regard some of their features as the result of extreme specialisation and even degeneracy. For the brain, at least, the statements made in the text appear to hold good (cf. Elliot Smith, "Origin of the Corpus Callosum," *Linn. Trans.* vii, Ser. 2), and to the brain-evidence much weight must admittedly be attached.

mammal-like Reptiles Cotylosauria and Therocephalia. The definiteness of this part of the history (also the absence of any suggestion of Amphibian relations), must be specially remarked. For in spite of their "mammalian" characters the omission of these particular Reptiles has been proposed. Of these characters the most important (on account of the preservation of the parts in fossil examples) relate to the joint between the lower jaw and the skull. Reference has been made already (p. 19) to this joint, and to the reduction of the quadrate bone in Mammals. The arrangement shewn in the diagram, placing the Permian Reptiles in the line of descent, commands a large balance of expert opinion. Hubrecht (1897) and Kingsley (1900) seem to be the most prominent of those who prefer to exclude these and more modern reptilian forms from a place in the line of Mammalian ancestry.

The Prototheria (Monotremata) are made to diverge even in the Triassic period, but this is a matter of speculation only, since the only extinct Prototherians known so far are derived from very late (Post-Tertiary) cave-deposits in Australia.

The point of divergence of the existing Orders of Marsupials (Diprotodontia and Polyprotodontia) is placed with confidence in the Jurassic period. After this comes an area in which the evidence is scanty and equivocal, marked by the indication "Undiscovered Placentals." But when this region of "Cretaceous uncertainty" has been passed, the early phases of the Tertiary period are marked by a perfect explosion of Eutherian forms. Here we are interested chiefly in a group to the right side of the diagram and the lines may now be traced from the periphery inwards. The Lemuroidea and Anthroproidea are there shewn to be joined as the Primates (not marked); the latter stem springs from a branch common to it and the Dermoptera (with the Cheiroptera) on the one side, and the insectivorous Tupaioides on the other. This common branch represents the Super-order Archonta (*v. supra*, p. 26), and its own origin is found almost at the root of all the Eutherian stocks.

Of the various Eutherian Orders, it thus appears that the Primates, Cheiroptera, Dermoptera, and Tupaioides (formerly a subdivision of the Insectivora, and now separated as the Order Menotyphla) are associated with the Insectivora (Soricoides, etc.) and

that the latter arise at the root of the limb common to the whole Eutherian Section (or Infra-class). The Edentate Orders (Tubulidentata and Xenarthra) are also placed close to that region¹. But the remainder are widely dispersed, and far removed from the root-stock. Special note should be taken of the distance separating the Artiodactyla and Perissodactyla, as well as that separating either or both from the Proboscidea, for all were formerly included in the heterogeneous assemblage called the Order Ungulata.

Complicated as all this may seem, a general acquaintance with the main outlines of the scheme is absolutely necessary before use is made of such a simplified "linear" substitute as is given in Fig. 16.

A few remarks are needed in justification of the expression (which recurs several times in the latter diagram) "stage of" such and such a "generalized" animal.

On the hypothesis of evolution, a given animal owns an ancestry including forerunners which would be classed as Reptiles possibly, or again as Amphibia, or as Fishes. Moreover in each Class, a generalized ancestral form is to be expected, i.e. a form which has not realized to the full the possibilities of specialization within its Class. The word "stage" is placed at the opening phase of each period. The ancestor at any stage would present such a combination of morphological characters as would lead to its being placed on the confines of two groups.

This digression is necessitated by the protest (made with vigour by some highly competent authorities²) against reference to "generalized" forms. An appeal in favour of specialized groups is substituted by those who thus object.

In revising my diagram, I was careful to consider whether it were misleading in view of that protest, the importance of which I recognize fully. I decided that the diagram is still reliable for the following reasons. In the first place, it does not exclude specialized forms from putting in an appearance during the course of progress denoted by the line joining the successive stages. Secondly, I think the "generalized" form must occur somewhere, sooner or later, in the genealogical tree. For instance the Reptile (without prejudice as to its specialization or the reverse) is more generalized than the Mammal, the Amphibian more generalized than the Reptile. If there be an objection to the diagram, I think it is to be found in the rectilinear character of the line of ancestry as drawn. But the diagram is submitted for

¹ Judged by the single criterion of brain-formation, this judgment appears from the researches of Elliot Smith (*Linn. Trans.* vii, Ser. 2) to need revision; for the neopallial part of the brain in some Edentata is more highly developed than in certain mammals commonly regarded as their superiors.

² Gaskell, *Origin of Vertebrates*, p. 497.

- * Stage of Primate mammal (Order Primates).
- * "Insectivorous" stage (Super-order Archonta).
- * Stage of generalized Eutherian mammal (Section Eutheria).
- * Stage of generalized Metatherian mammal (Section Metatheria).
- * Stage of generalized Therian mammal (Sub-Class Theria).
- * Stage of generalized Prototherian mammal (Sub-Class Prototheria).
- * Stage of generalized Mammal (Class Mammalia).
- * Stage of generalized Reptile (Class Reptilia).
- * Stage of generalized Amphibian (Class Amphibia).
- * Stage of generalized Fish (Class Pisces).

Fig. 16.

consideration after the more natural representation provided in Fig. 15, where the really tortuous nature of the several lines is sufficiently evident. The doctrine of "evolution from the most specialized" is so important in regard to the Phylogeny of Man, that its notification here is absolutely necessary, and it will be discussed further in the sequel. For the moment, the diagram submitted in Fig. 15 is to be regarded not as expressing all the facts of the case, but as the most convenient form of expression available¹.

The diagnostic characters of the Prototheria, given in Chapter II (p. 26), provide evidence of the lowly position assigned to those animals in relation to the other Mammalia. Some of the more important items are given in the following list.

- (1) The possession of oviducts which are distinct from each other throughout their course.
 - (2) The possession of a cloaca.
 - (3) The lack of vertebral epiphysial plates.
 - (4) The structure of the shoulder girdle (full development of the several elements).
 - (5) The production of meroblastic ova,
- as well as the physiological characteristic of being oviparous.

Turning now to the Metatheria (Marsupialia), the evidence for the lowlier status of these as compared with the Eutherian mammals depends chiefly on the conformation of the brain, which lacks the great cerebral commissure known as the corpus callosum; herein the brains of Metatheria (Marsupialia) resemble those of Monotremata and Reptilia, while differing from those of Eutheria. The mode of development of the embryo of some Metatheria provides additional evidence of the highest significance, viz. the relatively large size of the ovum and its enclosure by a shell membrane, discovered in the Marsupial *Dasyurus* by Professor J. P. Hill². These characters place the genus (*Dasyurus*) in a lowly position among the Metatheria. The genus *Perameles* also possesses primitive characters as compared with its associates.

Within the range of the Eutheria, the primitive characters (notably those of the brain) presented by the Insectivora have the

¹ For useful additional data in regard to such genealogical trees, v. Dendy, *Outlines of Evolutionary Biology*, Figs. 85 and 86.

² v. *Nature*, Oct. 22, 1908, p. 649, and the fuller account in *Q. J. M. S.* 1910.

effect of setting them in the lowest ranks. Among the members of the Order (Insectivora) the East Indian *Gymnura rafflesii* seems to combine almost the largest number of these lowly characters. Yet it is in this respect displaced by another East Indian competitor, viz. *Tupaia* and its allies. These (*ex. gr.* *Tupaia*) were formerly included in the Order Insectivora but are now segregated as the Order Menotyphla (cf. p. 26 *supra*). The following anatomical features testify to their lowly status:

1. The teeth: upper molars tri-tubercular¹; lower molars tuberculo-sectorial (*Tupaia*).

2. A (small) "tympanic" process of the alisphenoid (cf. Fig. 13 for this marsupial character) persists (*Tupaia*).

3. The organ of Jacobson is of the Marsupial type².

4. The scrotum is pre-penial, as in Marsupials, and on such facts are based the reasons for regarding *Tupaia* as the best living representative of a generalized Eutherian mammal. All the more significant is the claim recently made on its behalf, for admitting it into the Order Primates³.

Passing to the Order of the Primates, it will be necessary to set forth in detail the general morphological characteristics of the Order as well as those of its several subdivisions. The latter consist of Sub-orders, Families, Genera and Species, which may be grouped as follows.

Sub-order	{	Family Lemuridae (several genera and species).
LEMUROIDEA	{	Family Cheiromyidae (a single genus and species).
Sub-order	{	
TARSII	{	A single family (and genus; one or two species).
	{	Family Hapalidae (one genus; several species).
	{	Family Cebidae (several genera and species).
	{	Family Cercopithecidae " " "
Sub-order	{	Family Simiidae " " "
ANTHROPOIDEA	{	(? Family Pithecanthropidae; number of genera and species unknown: all the representatives are now extinct).
	{	Family Hominidae (one or two genera, and at most, three species, of which only one exists at present).

¹ Gregory, *op. cit.* 1910, p. 279. For the definition of tri-tubercular molar teeth v. *infra*, p. 283.

² Broom, *P.Z.S.* (abstract), April 13, 1915.

³ Kaudern, *Zoologische Jahrbücher*, 1910.

The first point for remark is the retention of the Sub-order Lemuroidea. Professor Hubrecht on the ground of the embryonic history and nutrition ("diffuse placentation") of the Lemuroidea, demands their rejection. Yet he would retain *Tarsius* among the Primates.

Professors Gadow and Elliot Smith are in favour of retaining the Lemuroidea and *Tarsius*, but they place the latter in an independent Sub-order, as shewn in the foregoing scheme. The arguments advanced by Professor Elliot Smith in favour of retention are based on observations directed to the anatomy of the brain. They may be summarised as follows¹:

Cerebral characters indicative of the appropriateness of retaining the Lemuroidea within the Order Primates².

1. The Lemuroidea agree with the Anthropeidea and differ from all other Eutheria in the possession of a true Sylvian fissure.
2. The sulcus centralis is actually present in the lemurine *Perodicticus*; it occurs in no non-primate mammal, nor in the other Lemuroidea, although in these a tendency exists to the development of a furrow limiting caudally the motor area (as does the sulcus centralis).
3. The motor area of the cortex resembles histologically that of the Anthropeidea and has a similar topographic distribution.
4. The sulcus calcarinus and the distribution of the visual area conform precisely to the type found in the Anthropeidea, though in some respects affinities to the Carnivora are shewn.
5. The characters of the cerebellum present corresponding resemblances to those met with in the Anthropeidea.
6. The evidence nevertheless assigns to the Lemuroidea a lowly position in the Order Primates.

The second point to be discussed is the dissociation of the *Tarsii* from the Lemuroidea. The former provide several interesting links between the Lemuroidea and the Anthropeidea, as will be explained in the sequel (p. 105). The Family Pithecanthropidae is a provisional one, and to it are referred (a) the Javanese fossil remains called *Pithecanthropus erectus*³, and (b) the Mauer jaw from Heidelberg³.

Within the Hominidae, the cranial fragments recently discovered (1912) by Messrs Smith-Woodward and Dawson in Sussex (the Piltdown skull) are claimed as distinctive of a separate genus (*Eo-anthropus dawsoni*), while the

¹ The following memoirs should be consulted:

1. Elliot Smith, *Lim. Trans.* vol. viii, Part 10, p. 417.
2. " *Lin. Soc. Journal*, vol. xxix, pp. 80—89.
3. " *Nature*, 1907, May 2, p. 7.
4. " *Brit. Assoc. Report*, 1908, p. 875.
5. " *Nature*, 1909, p. 88.
6. Standing and Elliot Smith, *Zool. Trans.* vol. xviii, Part 2, 1908, p. 59.

² Elliot Smith. No. 3 of preceding note.

³ v. Chapter xvii.

Neanderthal skeleton and its congeners probably represent forms specifically distinct from *Homo sapiens*. The fuller consideration of these extinct types is reserved however for a later chapter (xvii).

It is now convenient to enumerate the diagnostic characters of the various Sub-orders of the Primates. For this purpose, the concise statements made by Professors Parker and Haswell (in their *Textbook of Zoology*) have been drawn on freely (with permission).

Order Primates: Eutheria, nearly all of which are adapted to an arboreal life, the limbs being prehensile owing to the pollex and hallux being more or less completely opposable to the other digits.

Dentition: heterodont; diphyodont; incisor teeth two in number on each side above and below: the Aye-Aye (*Cheiromys*) and Tarsii are exceptions to this rule.

Digits: are, in nearly all, five in number, and are provided with flat nails both in manus and pes: the pollex and hallux are opposable.

Forearm: the ulna and radius are separate (*i.e.* not ankylosed as in many Eutheria) and well developed.

Orbit: surrounded by a bony ring.

Clavicles: well developed.

Entepicondylar foramen: abnormal (Parker and Haswell say absent).

Third trochanter of femur: abnormal (Parker and Haswell say absent).

Stomach: simple in most instances.

Testes: descend into a scrotum.

Mammae: usually two in number, and thoracic in position.

Placenta: variable (diffuse or meta-discoidal).

SUB-ORDER

LEMUROIDEA

Ape-like Primates, nocturnal in habit, and of comparatively low organisation. (Cf. Fig. 17.)

Teeth: dental formula $i, \frac{2}{2}; c, \frac{1}{1}; pm, \frac{3}{3}; m, \frac{3}{3}$; the upper median incisor teeth are widely separated in most cases.



Fig. 17. General external appearance of a Lemur. (Adapted from Mitchell, *Childhood of Animals*.)

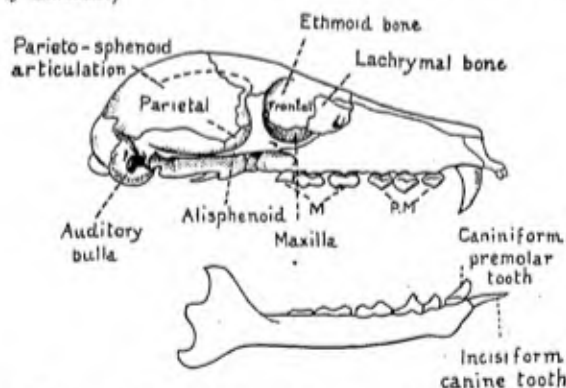


Fig. 18. Cranium, with mandible, of *Lemur varius*; note the auditory bulla, the articulation of parietal and alisphenoid bones, the facial extension of the lachrymal bone (cf. Fig. 21), the articulation of the frontal bone and maxilla behind the lachrymal bone, the small forward projection of the orbital plate of the ethmoid bone, the number of teeth, the small size of the upper and the great projection of the lower incisor teeth. In the mandible, the canine-like tooth is a pre-molar by position, and the canine tooth is incisiform.

Digits: of fore and hind limbs bear flat nails except the second digit of the hind limb, which bears a claw. Both pollex and hallux are opposable.

Orbit: surrounded by a bony ring. (Cf. Fig. 18.)

Lachrymal foramen: external to orbit.

Hyoid bone: anterior larger than posterior cornu.

Colon: "bent on a bight" in its transverse portion. (Cf. Fig. 19.)

Cerebral hemispheres: feebly convoluted and not prolonged far backwards over cerebellum (Fig. 44): rhinencephalon relatively well-developed.

Mammæ: two in number, thoracic in position; they may be supplemented by an abdominal pair.

Uterus: bi-cornuate.

Placenta: diffuse.

The Sub-order Lemuroidea comprises the true Lemurs (Family Lemuridae), so called from their ghost-like appearance at night. Geographically, their distribution is almost entirely confined to the island of Madagascar,

in which they have found congenial surroundings; and of the local fauna they are very characteristic. A few examples occur in Africa and Asia. Fossil representatives occur, not in Madagascar only, but also in Europe and in North America.

The arboreal animal known as the Aye-Aye, *Cheiromys* or *Daubentonia madagascariensis* is, as its name indicates, a Malagasy representative. It is so peculiar as to have been assigned to a

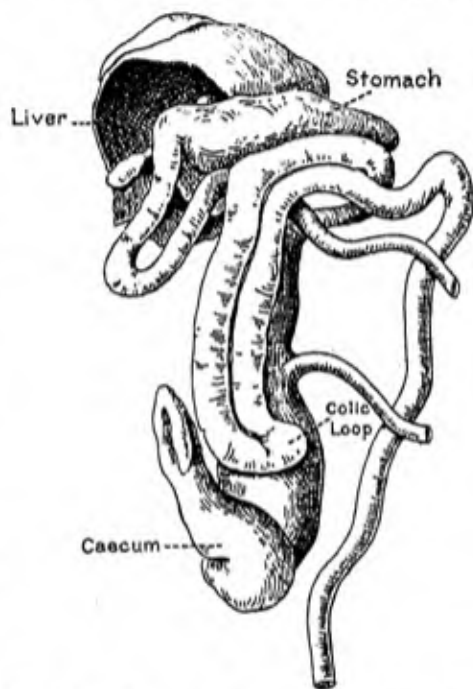


Fig. 19. Part of the alimentary canal of a Lemur: note the curiously contorted colon, and the enormous appendix caeci.

separate family, of which it constitutes the sole living genus and species. At first its relation to the Lemuroidea was not recognized, chiefly because its incisor teeth simulate those of a rodent. But when its general anatomy became known, the evidence thus obtained clearly shewed its affinities with the Lemurs, and with these it now finds a place in classification. It is to be regarded as an exceptional form of the particular lemurine type known as the Indrisinae. It can be described justly as a "specialized" form, though in its case specialization is compatible with, and may indeed be evinced by, certain features (such as those of the brain) which can only be termed "degenerate."

SUB-ORDER

TARSII

Very diminutive arboreal Primates, nocturnal in habit (Fig. 20).

Teeth: dental formula $i, \frac{2}{1}; c, \frac{1}{1}; pm, \frac{3}{3}; m, \frac{3}{3}$; the upper median incisor teeth are in contact.

Digits: provided with round sucker-like discs: nails flat save on the second and third toes, which bear sharp claws.

Orbit: a post-orbital wall is present.

Lachrymal foramen: external to orbit.

Hyoid bone: "lesser" cornu longer than "greater" cornu, but consisting of three ossified portions with cartilaginous intervals.

Colon: not bent as in Lemurs.

Cerebral hemispheres: feebly convoluted; prolonged further backwards than in the typical lemurine condition; rhinencephalon relatively small.

Mammæ: four in number, of which two are pectoral, and two inguinal in position.

Uterus: bicornuate.

Placenta: discoidal.

This Sub-order comprises the genus *Tarsius* with two species, or, it may be, varieties. These are found in a comparatively circumscribed geographical area, viz. the islands of the Eastern Archipelago from Sumatra to the Philippine group. The fossil *Anaptomorphus* found in North America is considered to be nearly related to *Tarsius*.



Fig. 20. *Tarsius spectrum*, a representative of the Sub-order Tarsii (the figure is slightly less than the life-size of the animal).

SUB-ORDER ANTHROPOIDEA

Most highly organised Primates, chiefly modified for and adapted to an arboreal mode of life.

Teeth: the upper median incisor teeth are in contact with one another.

Digits: these are provided with flat nails (except in the Hapalidae).

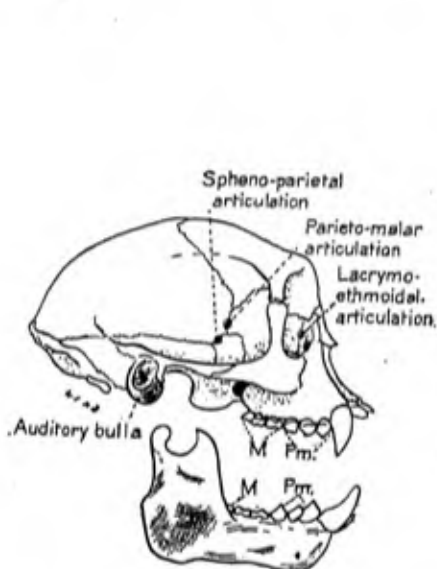


Fig. 21.



Fig. 22.

Fig. 21. Cranium, with mandible, of *Cebus capucinus* (Cebidae). Note the auditory bulla, and shallow auditory passage; the spheno-parietal and lacrymo-ethmoidal articulations, the latter suture being marked by a small circle; three molar teeth are seen in each jaw.

Fig. 22. Part of the alimentary canal of a *Cercopithecus* monkey (Cercopithecidae); note the lack of contortion in the colon, and the absence of an appendix caeci.

Pollex: in a few instances is rudimentary or absent, in most it is well developed.

Orbit: the post-orbital boundary is a bony wall extending inwards from the post-orbital ring, and separating the orbit from the temporal fossa. (Cf. Fig. 21.)

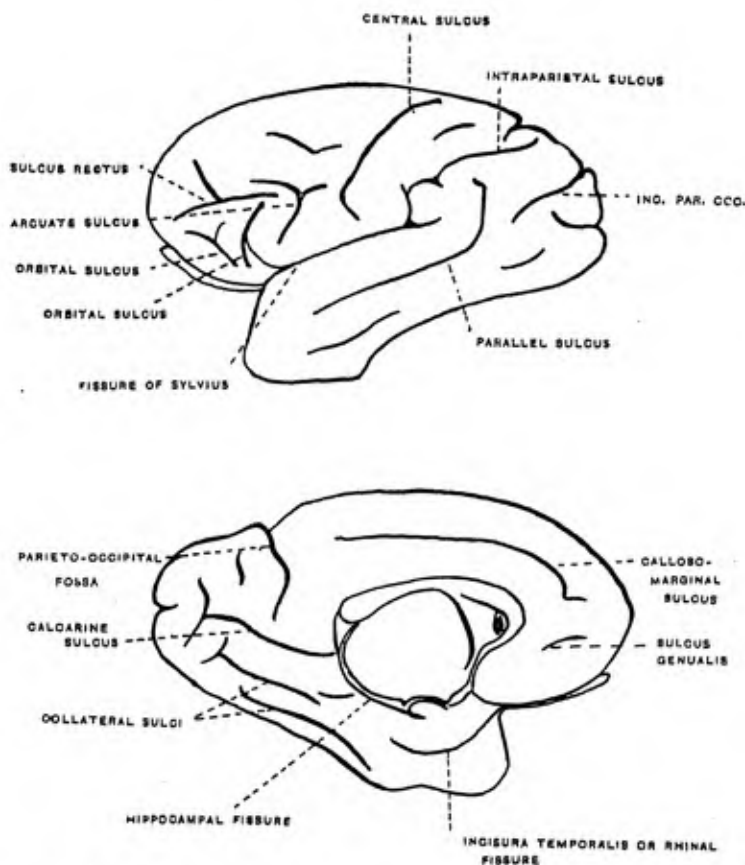


Fig. 23. The left cerebral hemisphere of an American (Platyrrhine) ape, *Ateles variegatus*: the lateral and mesial aspects of the hemisphere are shown. (Mus. Anat. Cant.)

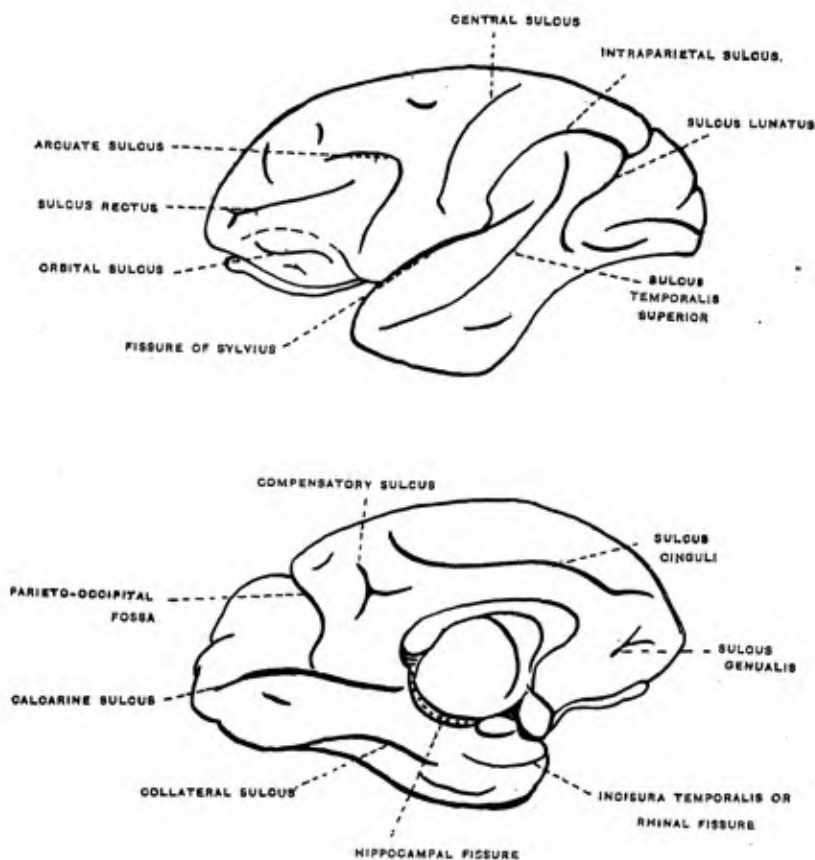


Fig. 24. The left cerebral hemisphere of a *Nasalis* monkey (*Cercopithecidae*): the lateral and mesial aspects are shewn. (Hose Donation II. Mus. Anat. Cant.)

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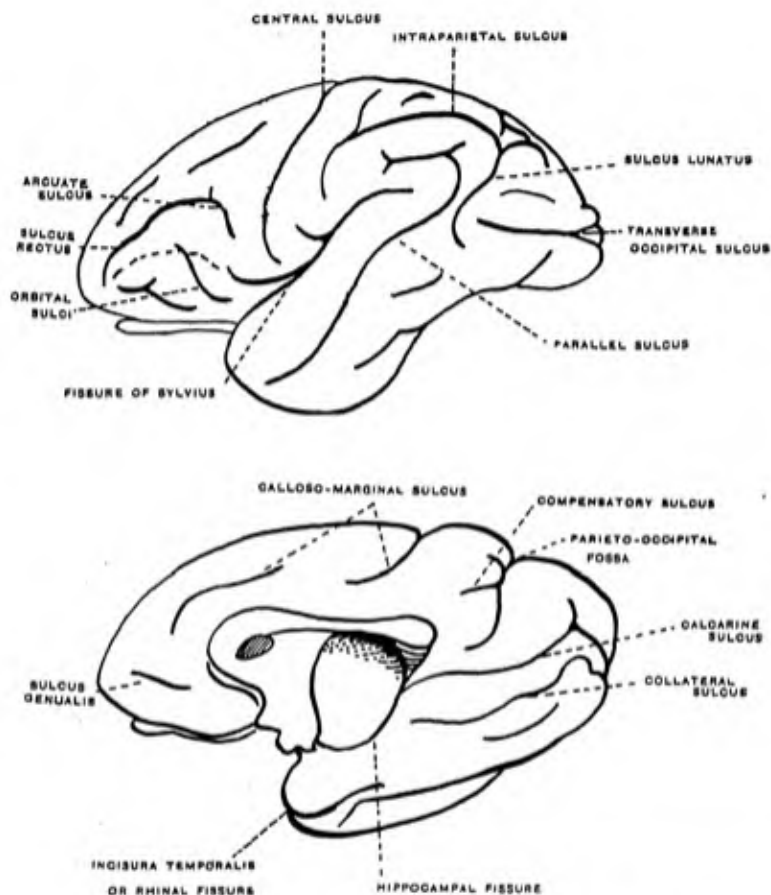


Fig. 25. The cerebral hemispheres of a Gibbon (Simiidae): the lateral and mesial aspects are shown. (Hose Donation II. Mus. Anat. Cant.)

Lachrymal foramen: this is situated within the orbital margin.

Hyoid bone: the posterior cornu exceeds the anterior cornu in size.

Colon: not looped as in Lemuroidea. (Cf. Fig. 22 with Fig. 19.)

Brain: cerebral hemispheres much convoluted and prolonged backwards to cover the cerebellum to a considerable extent (Figs. 23, 24 and 25): rhinencephalon much reduced.

Mammæ: two in number and thoracic in position.

Uterus: this has no cornua properly so called: Fallopian tubes spring directly from the body of the uterus.

Placenta: this is deciduate and meta-discoidal.

Family I. Hapalidae¹.

Dental formula: $i, \frac{2}{2}$; $c, \frac{1}{1}$; $pm, \frac{2}{2}$; $m, \frac{2}{2} = 32$.

Pollex: not opposable.

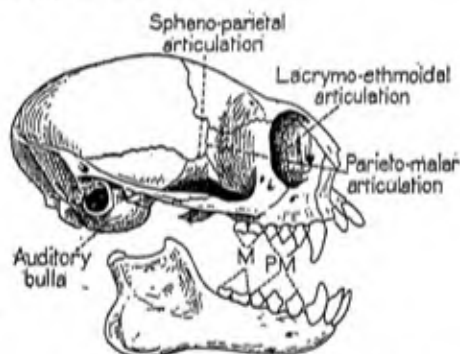


Fig. 26. Cranium, with mandible, of *Hapale jacchus* (Hapalidae). Note the auditory bulla, the sphenoparietal articulation and in the orbit the lacrymo-ethmoidal articulation; two molar teeth are seen in each jaw, and the incisor teeth project strongly (\dagger).

Digits: bear claws, no nails: the hallux is an exception to this rule.

Cheek pouches: not developed.

Ischial callosities: not developed.

External auditory meatus: not prolonged into an osseous tube. (Cf. Fig. 26.)

¹ (Hapale: from a Greek word indicative either of minute size, or docile temperament.)

Tail: non-prehensile.

Nasal septum: wide (Platyrrhine).

The foregoing family includes the Marmosets.

*Family II. Cebidae*¹.

Dental formula: $i, \frac{2}{2}; c, \frac{1}{1}; pm, \frac{4}{4}; m, \frac{3}{3} = 36$.

Pollex: not opposable, in some instances rudimentary or absent².

Digits: all have flat nails.

Cheek pouches: not developed.

Ischial callosities: not developed.

External auditory meatus as in Hapalidae (cf. Figs. 21 and 26).

Tail: sometimes prehensile.

Nasal septum broad (Platyrrhine).

This family includes among others the Howling Monkey (Mycetes), Squirrel Monkey (Chrysothrix), Spider Monkey (Ateles), and Capuchin Monkey (Cebus).

It should be particularly noted that members of the two preceding families (Hapalidae and Cebidae) agree in the possession of a wide septum and space between the nostrils. They are for this reason called Platyrrhine Monkeys. Besides this characteristic, other morphological features distinguish the Platyrrhine apes from the other Anthropeida, which from the possession of a narrow intra-narial space and consequent downwardly directed nostrils are called Catarrhine. In Craniology the term Platyrrhine is also used, but there it refers to the proportions of the apertura pyriformis nasi of the skull, and not to the intra-narial space of the face.

*Family III. Cercopithecidae*². (Cf. Fig. 27.)

Dental formula: $i, \frac{2}{2}; c, \frac{1}{1}; pm, \frac{2}{2}; m, \frac{3}{3} = 32$.

Pollex: opposable (but in the genus *Colobus* not developed at all).

¹ (Cebus: the Arabic word for ape.)

² For a striking human example of congenital absence of both thumbs (including the scaphoid and greater multangular bones) see Dr Sequeira's account in the *Lancet* (1913, Feb. 8, p. 386).

³ (Cercopithecus: a tailed ape.)



Fig. 27. An adult male *Nasalis* or Proboscis monkey; a variety of *Semnopithecus* (*Cercopithecidae*) from Borneo. (Hose Donation, No. II. Mus. Anat. Cant.)

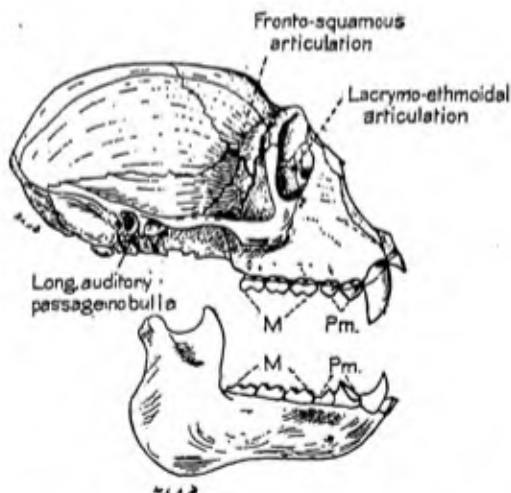


Fig. 28. Cranium, with mandible, of a *Macacus* monkey (*Cercopithecidae*); note the absence of an auditory bulla; the substitution of fronto-squamous and fronto-maxillary for sphenoparietal and lachrymo-ethmoidal articulations: note also the number of teeth, and compare with Figs. 21 and 26.

Cheek pouches: developed in many cases.

Ischial callosities: developed to a high degree.

External auditory meatus: guarded by an osseous tube formed by the tympanic bone. (Cf. Fig. 28.)

Tail: non-prehensile.

Nasal septum: narrow anteriorly, the nostrils close together in consequence.

Sternum: narrow and rod-like.

Caecum: has no vermiform appendix.

This family comprises the Baboons (*Papio* or *Cynocephalus*), the Macaques (*Macacus*), the *Cercopithec*i, *Semnopithec*i, etc.

*Family IV. Simiidae*¹. (Cf. Figs. 29, 30, 31.)



Fig. 29.



Fig. 30.



Fig. 31.

Fig. 29. Adult male Gorilla (*Simiidae*); the hair has been lost owing to inadequate preservation in alcohol. (Holt Donation, Mus. Anat. Cant.)

Figs. 30 and 31. Other views of the same specimen.

¹ (*Simia*: exact meaning doubtful; either "flat-nosed" or "mimic.")

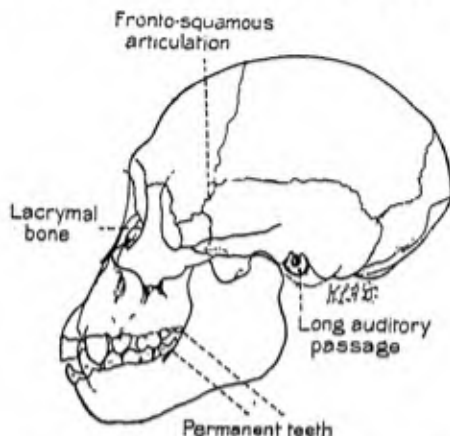


Fig. 32. Cranium, with mandible, of a young Gorilla (*Simiidae*); the first tooth of the permanent set has appeared (permanent molar tooth). Note, in contrast to Fig. 33, the comparatively large brain-case. There is no auditory bulla: the auditory passage is long, but not so long as in adults: there are fronto-squamous and fronto-maxillary articulations. Osseous ridges and crests are still undeveloped.

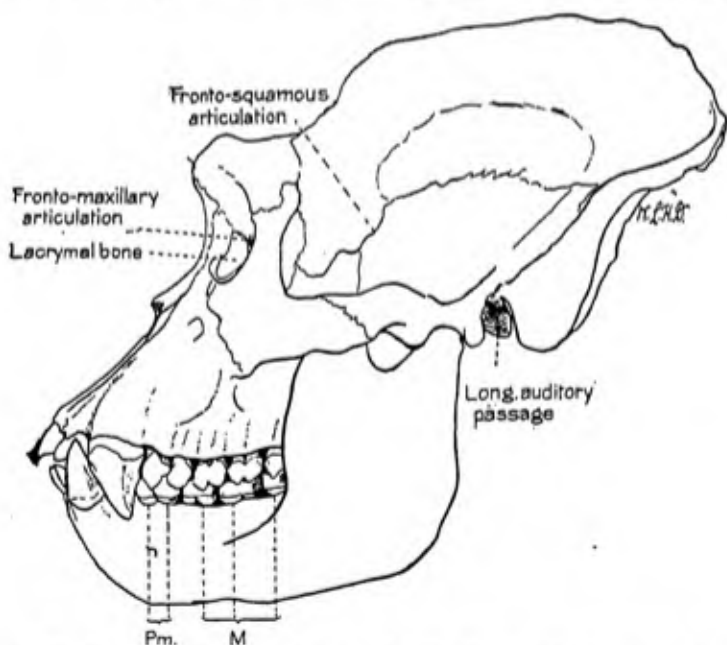


Fig. 33. Cranium, with mandible, of an adult Gorilla (*Simiidae*): note the absence of an auditory bulla, the presence of great bony crests; and of fronto-squamous and fronto-maxillary articulations (the latter within the orbit in place of a lacrymo-ethmoidal junction). The canine teeth are enormously developed in the male sex.

Dental formula: as in the preceding family, viz.:

$$i, \frac{2}{2}; c, \frac{1}{1}; pm, \frac{2}{2}; m, \frac{3}{3} = 32.$$

Pollex: opposable.

Ischial callosities: found in one genus only, viz. *Hylobates* (the Gibbons).

External auditory meatus: an osseous tube, as in Family III. (Cf. Figs. 32, 33.)

Tail: not developed externally.

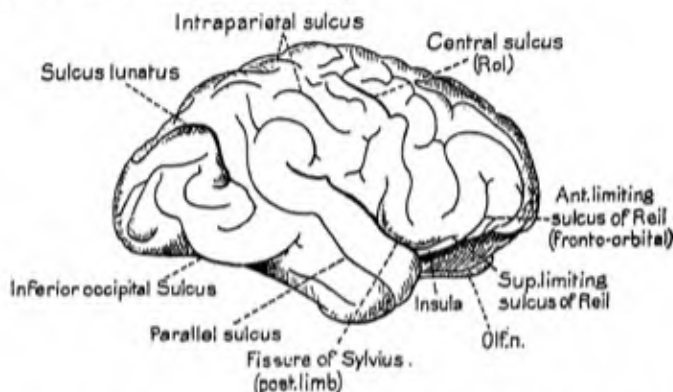


Fig. 84. Lateral aspect of the right cerebral hemisphere of a young Gorilla (*Simiidae*). The olfactory nerves are attenuated in point of size: the cerebral surface is much more convoluted than in the preceding examples and recalls the appearance of the human cerebrum. Cf. with Figs. 23, 24, 25, 44, and p. 46.

Nasal septum: as in Family III.

Sternum: flat (lati-sternal type).

Caecum: vermiform appendix present.

Os centrale carpi: sometimes united with the os radiale carpi to form the scaphoid bone.

This family includes the Gibbons (*Hylobates*), Orang-utans (*Simia*)¹, Chimpanzees and Gorillas (*Anthropopithecus niger* and gorilla).

Family V. Hominidae.

The main characters conform so exactly to those of the preceding family that recapitulation is unnecessary. The Hominidae are however distinguished from the Simiidae by several morphological characteristics of which the following are the most important.

¹ For the latest revision of these names, v. *infra* p. 158, footnote.

Hallux not opposable.

Pelvic limbs much longer and bulkier than the pectoral.

Cerebral hemispheres enormously developed in bulk and in the complexity of the convolutions.

Many morphological modifications have been induced by the assumption of the erect attitude.

This family includes members of the two Human species.

It is a matter for discussion whether there should be interpolated between the Families Simiidae and Hominidae another, viz. Pithecanthropidae. Till further remains of Pithecanthropidae have come to light this question must remain in abeyance. Some authors would rank Pithecanthropus erectus with the Simiidae, and others again associate this form with the Hominidae.

In concluding the account of the Order Primates, a few words may be added as to the method pursued in assigning to Man a place among the Mammals. It will have already been noticed that in the account given of the Order Primates, several morphological characters were enumerated. Should a mammal be presented for examination with a view to assigning it to its appropriate order, it would be necessary that the mammal should satisfy the conditions just referred to, before such assignation could be made in respect of the Order Primates. But the exact number of conditions is a matter upon which no final decision has been arrived at. It is conceded very generally that the decision should not depend on a single character. And however desirable it may seem, to limit the number of tests for the sake of convenience and lucidity, no hard-and-fast rule (as to the precise number of tests) can be formulated. An example of the procedure may facilitate this explanation. We may for instance consider the morphology of a typical Primate mammal and enumerate a dozen characters in which it presents the requisite conformation. The corresponding list for the human body would shew that the same conditions were satisfied in this as in the preceding case. Closely similar results would follow the application of the test to the various animals just mentioned, and it is in this way that the constitution of the Order Primates has been effected. Nevertheless, difficult cases occur, and one of these has been selected by way of illustration. Should we be confronted by such a form of mammal as *Galeopithecus volans* (which was included among the Primates at an epoch when the single character of the possession of two incisor teeth in each jaw was regarded as the sole qualifying condition), we should see but small reason at first for regarding it as outside the limits of that Order.

The comparison may be drawn up as follows, the selected characters including nine of the most important of those already employed (in the general diagnosis of the Primates, cf. p. 44 *supra*).

Characters	Homo sapiens	Typical Primate of the Lemnoid type	Galeopithecus volans
Dentition	Dental formula $\frac{2.1.4.3}{2.1.4.3}$; molars broad; angles rounded; no transverse ridges; no talon	Dental formula $\frac{2.1.4.3}{2.1.4.3}$; lower canines incisiform; molars tri-tubercular; talon present	Dental form. $\frac{2.1.4.3}{2.1.4.3}$; crowns of lower incisors are pectinated; the canine and outer incisor have double roots
Orbital region of skull	Bounded posteriorly by a post-orbital wall	Bounded posteriorly by a post-orbital bar	Post-orbital processes; no bar or wall
Clavicle	Well developed	Well developed	Well developed
Forearm bones	Independent; pronation and supination occur	Independent; pronation and supination occur	Distally united
Carpus and digits	Five digits; os centrale carpi not separate	Five digits; os centrale distinct	Five digits; os centrale carpi not separate
Cerebrum	Large and much convoluted	Small and feebly convoluted	Small and almost smooth
Uterus	Simple; not bicornuate	Bicornuate	Bicornuate
Stomach	Simple; not sacculated	Simple; not sacculated	Simple; not sacculated
Cæcum	With Appendix	No Appendix	With Appendix
Mammæ	Two in number; pectoral in position	Often two pairs, viz. one pectoral pair, one inguinal pair	Two axillary pairs of mammae
Testes	Scrotal	Scrotal	Scrotal
Pollex	Freely opposable	Freely opposable	Non-opposable
Placenta	Disc-like	Diffuse	Disc-like
	[This combination of characters qualifies the animal for admission into the Order Primates]		
	[This combination of characters does not qualify the animal for admission into the Order Primates]		

This table shews a majority of points of agreement as between *Galeopithecus volans* and the typical Primate mammal. Evidently there is a certain degree of affinity between the two forms. But the characters in which they are contrasted are not a small minority, and although by extending the list other features of similarity may be added, the points of contrast become more numerous and striking. Above all, perhaps, the possession of a patagium suggests forcibly some approach to the Cheiroptera. Yet when the comparison is instituted with these (the Bats) in details, *Galeopithecus* appears as an aberrant representative of the Order Cheiroptera, just as it has figured as an anomalous member of the Primates. The discovery of yet other characters in turn suggestive of the Insectivora (Menotyphla) complicates the matter further. Yet if a classification must be made, it is necessary to draw lines somewhere or other. In this instance, some systematists have solved the problem by instituting an independent Order (Dermoptera) for *Galeopithecus volans*, which is compensated thus for the loss of its claim to the title of "Flying Lemur."

If it is difficult to prescribe the exact number of characters to be employed in such tests, the question as to their precedence is equally hard to solve. At present no general consensus of opinion seems to exist as to the order of importance in which such characters as those used in the foregoing table (p. 60) are to be arranged. It is submitted, however, that the list contains none but characters of the most valuable kind, no matter how their sequence may be adjusted. And if the teeth and skeleton appear too highly placed, let it be remembered that of fossil animals such parts alone remain in many instances. Moreover the cranium even in fossil forms is often capable of providing information as to the cerebrum itself, if endocranial casts can be prepared. As for the central nervous system in general and the brain in particular, their high value in these researches is so widely recognized now, that the mere mention of them will suffice in this connection¹.

We have thus given a general idea of the position of the Hominidae within the Order Primates. In order to strengthen the argument for assigning to Man this position, a more detailed exposition of the anatomical characters of the Primates seems advisable. For this reason we have selected as examples of the Order (a) one of the Lemurs, (b) *Tarsius spectrum*, (c) one of the Cercopithecidae, and (d) one of the Simiidae. The anatomy of each of these will be briefly reviewed (Chapter IV), and

¹ For an admirable chapter on the choice of criteria and their relative value in evidence, cf. Gregory, "The Orders of Mammals," *Bulletin of the American Museum of Natural History*, 1910. Part II. Introduction.

arranged in a manner suitable for comparison with descriptive human anatomy, which is here excluded for lack of space. To these descriptions will then be added (Chapter v) detailed accounts of the skulls of the most nearly related family to the Hominidae, viz. the Simiidae. The dentition of the same families will also be described separately (Chapter vi).

CHAPTER IV

ON THE GENERAL ANATOMY OF THE PRIMATES

I. LEMUROIDEA.

IN the chapter dealing with the subdivisions of the Order Primates, the characters which have proved of taxonomic value in distinguishing the Sub-order Lemuroidea were enumerated. The following account provides a few additional facts descriptive of the anatomy of such a representative of the Sub-order, as for example *Lemur mongoz* (*seu fuscus*¹).

The selection of a really typical form of Lemur is not altogether easy, owing to the variability in size and dimensions met with among these animals. An enquiry into the general natural history of the Lemurs will lead quickly to the conclusion that the Sub-order (Lemuroidea) includes examples of specialization carried out in several directions and to very different degrees. In point of size, the Lemurs can shew a range of forms from the rat-like *Chirogale* (or *Mouse-Lemur*) to the *Indris* (relatively a giant type), which is comparable to a large terrier. Adaptation to environment differs: thus we may contrast the more purely arboreal forms (which predominate) with others found on rocky and almost treeless plains (*Lemur catta*). The length of the tail is another very variable feature. Some Lemurs (such as the *Galagos*) can progress in the bipedal fashion of a *Jerboa* or *Kangaroo*, i.e. by leaps, while the large *Indris* assumes and maintains the erect attitude without difficulty². The colour of the furry coat provides the most striking contrasts; in some instances wide variations occur within the limits of a single species. There are nocturnal

¹ Cf. Forsyth Major, *P. Z. S.* 1901, March 19.

² Flacourt (quoted by Hubrecht) asserted this also of *Propithecus*.

and diurnal groups: omnivorous and herbivorous forms: some types hibernate, though these are exceptional. The numbers of teeth and of the carpal bones are not absolutely constant throughout the Sub-order.

But although such diversity of form and habits must not be overlooked, it is still true that a large number of Lemurs agree in certain general characters. Such a group may fairly be called typical, and from it the present selection must be made. It is perhaps noteworthy that the very fact of such variability is of itself suggestive that the Sub-order provides materials from which, in the course of Evolution, higher types may be reasonably supposed to have arisen whether through Natural Selection or otherwise. At the same time, it is not necessary to suppose that the "true Lemurs" represent exactly the particular varieties thus favoured and consequently figuring in the ancestral history of the higher Primates. Indeed the opinion has been expressed (Forsyth-Major, Standing) that so far from advancing, many of the existing types have degenerated, from more highly-organised ancestors. However this may be, the choice of an example for descriptive purposes will fall advisedly on a specimen of the so-called "true" or typical Lemurs, which is described in the following paragraphs.

I. General considerations.

In the morphological study of the Lemurs, attention must be directed to the facts (i) that they constitute a relatively primitive group of Eutherian mammals, (ii) that they are quadrupedal, (iii) that they are arboreal and nocturnal in habit, (iv) that they are in diet usually insectivorous or omnivorous. It is probable that in reference to these considerations will be found the interpretation of all their salient structural characters. These will be found arranged in sequence either according to the various anatomical systems described, or in certain instances with reference to regions of the body.

II. Systematic description.

A. External characters. The commonest type of Lemur resembles in size a cat, and, as in that animal, the tail is long (Fig. 17). To its relatively small size and also to its nocturnal

habits are attributable the thick felt-like or woolly covering¹ of hair distributed over the body and the tail. The latter is not prehensile in the strict sense of that term, but nevertheless it can be twined round a bough to support the animal: it also plays an important part in balancing the animal during its arboreal movements. The nostrils are directed forwards as well as outwards, and the space between them is narrow (as compared with its width in Tarsius). The elongated snout and lower jaw are distinctive, as are the very large eyes with their circular pupils. The external ears are also large and capable of much movement. The prominence of eyes and ears is in accord with the nocturnal mode of life. The fore and hind limbs are of nearly equal length (a primitive and quadrupedal character), while the hands and feet are evidently and specially adapted to the prehensile functions so necessary to an arboreal animal.

B. The Hair. The peculiar (woolly) character of the hair in Lemurs renders difficult a definite separation of the several hair-tracts in adult examples. In miniature and foetal specimens, the mode of distribution of the hair is more clearly shewn. It has been described with great precision by Professor Schwalbe². In general it appears that in several noteworthy points the Lemurs present a modified form of the condition assumed to be most primitive, viz. that characterised by the uniform flow of the hairs from the tip of the nose backwards to the end of the tail. In regard to details, the groups of vibrissae (sinus-hairs) first require notice. In the Lemurs, these hairs are arranged in five groups. Of these, four are facial, and according to their situation are distinguished respectively as the supra-orbital, naso-labial, zygomatic and mental series. They are distinguished further not only by their length and rigidity, but also by a tendency to implantation in definite and circumscribed eminences or pads (one for each group). These pads are often more darkly pigmented than the surrounding skin. [The *submental* group of vibrissae

¹ Specimens of *Lemur catta* passed the winter of 1912—13 in the open air near Cambridge, without shewing any untoward effects of climate.

² *Über die Richtung der Haare bei den Halbaffen*. Sonderabdruck aus Voeltzkow *Reise in Ostafrika in den Jahren 1903—1905*, Band iv. 1910, from which publication Figs. 35, 36, and 37 have been taken with the author's permission.

found in certain rodents and insectivores, is said to be wholly unrepresented among the Lemurs.] The fifth group of vibrissae is on the forearm and near to it a cutaneous callosity may be seen in some varieties¹.

The eye-lashes arise not from the margin of the eyelid but from its external aspect.

As regards the general hair-covering², the direction of the

¹ Bland Sutton and Beddard. Cf. *Nature*, Jan. 9, 1902, p. 222.

² The arrangement of the hair-tracts in the mammals generally, and particularly in the Primates, possesses an extensive literature. To the valuable memoir by Schwalbe on the Lemurs (cf. footnote p. 65) must be added a subsequent and more exhaustive monograph on the Anthropoidea by the same author, by whom a full bibliography is provided (Schwalbe, 1912, "Über die Richtung der Haare bei den Affen-Embryonen," Selenka's *Studien über Entwicklung*, u.s.w., zehnte Lieferung). A notable feature of this work is the presentation of the author's views as to the general significance of the marked variations in the details of hair-tracts in reference to their direction and distribution. This subject has been studied also by Dr Kidd, who in 1903 published an account of his work (*The direction of Hair in Animals and Man*, 1903). Both authors agree in assuming the existence of a primitive type of distribution, such as that described above (p. 65) in which the hair is directed uniformly backwards (cranio-caudally) from the nose to the tail. This primitive and simple distribution has undergone many modifications in different animals. Dr Kidd invokes the influence of a number of mechanical causes, such as the action of gravity (cf. the Sloth), the habitual assumption of certain attitudes, or repetition of movements, and finally the relation to points called "fixed" as regards the action of subjacent muscles. To complete this account, it is necessary further to postulate a purely Lamarckian transmission of acquired characters. Professor Schwalbe, in rejecting these views, lays stress on three capital factors as accountable for the majority of the observed phenomena. Thus reference is made to (i) the occurrence of flexions (Faltungen) as at the throat, elbow or knee, when the hairs on either side of the angle will grow in the lines of least resistance and produce consequently divergence from or convergence towards a point. Again (ii) a localised depression of the skin, in conformity with the growth of the local tissues, will be followed by an analogous re-arrangement of the primitive tracts. Finally, (iii) the mode of increase in the surface area of the skin, and of the epidermis in particular, is evidently not uniform all over the body. Professor Schwalbe shews by an ingenious model that if such irregularity be granted, the production of hair-tracts in definite directions is a necessary consequence. (This part of Professor Schwalbe's position is not unlike the view expressed originally by Voigt.)

Professor Schwalbe thus throws back the basis of an interpretation of hair vortices, spirals, etc. upon the phenomena of growth, whereby folding and other irregularities of surface are produced. Many factors enter into these phenomena, such as the mode of life and consequent modifications in the details of form. At this point there seems to be an approach to the position adopted by Dr Kidd. Yet the latter, as we have seen, postulates causes acting directly from without, whereas

hairs on the head may be noted first. In the Lemurs, the hairs are directed from the brows backwards (cranio-caudally); but they encounter an opposing stream just before they have attained the region above the top of the ear (Fig. 35). This opposing stream ascends from twin centres (Fig. 36) placed symmetrically on each side of the nape of the neck.

A spiral centre of dispersion on each side of the abdomen is another characteristic feature of the Lemurine hair. At the elbow (Fig. 37), the convergence of hairs from the arm and forearm respectively is a character common to the Lemurs and many other mammals, including Man himself.

Specimens of Lemurs¹ in the Cambridge Anatomical Collection shew hairs distributed on the back (dorsal surface) of each finger and toe: in the pollex and hallux the distal phalanx is not thus covered: the hairs on the other digits extend to the nails.

In conclusion, it may be remarked that the hairs are commonly implanted in groups consisting of more than three hairs². This arrangement is of interest in relation to that of the hairs in certain scale-covered animals, supposed to indicate the descent of mammals from scale-clad ancestors.

C. **The skin** (in specimens doubtfully referred to *L. mongoz*) is of a dull slate-grey colour where exposed as near the nose, and on the hands and feet.

Professor Schwalbe appeals to the details of muscular development, or to variations in the proportions of different parts, which are only indirectly affected by the external agents suggested above. And such indirect influence is here held to be more probable than the alternative. In particular, it is thought that Professor Schwalbe is especially helpful when he calls attention to the necessity for considering the precise form of the surface to be provided with a hairy covering. This aspect of the problem will fall within the province of a geometrical analysis such as has been applied to the cutaneous surfaces of the palms and soles by Kolossof and Pankul (*Morphologisches Jahrbuch*, xxxv. 1906). These authors point out the existence of certain "neutral points" in any area of skin which is liable to changes in its surface form. During such changes, the neutral points escape the effects of tension or pressure necessarily felt by other points on the surface. It may well be the case that such points are suitable for the hair-bulbs, and that the grouping of the hairs is determined by their relative positions (*v. infra* in connection with hair-tracts).

¹ The species is undetermined, but is probably *L. mongoz*.

² Cf. Meijere, *Morphologisches Jahrbuch*, Band xxi. 1894.

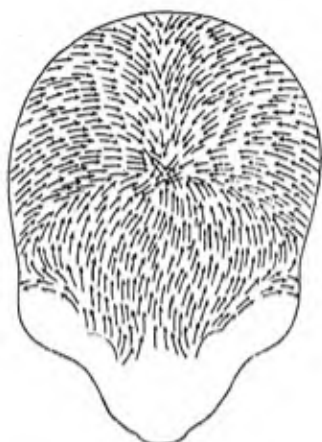


Fig. 35.



Fig. 36.



Fig. 37.

Fig. 35. Lemur mongoz (embryo). Hair-tracts of the head. (From Schwalbe, *op cit.*)

Fig. 36. Lemur mongoz (embryo). Hair-tracts of the dorsal aspect of the head and trunk. (From Schwalbe, *op. cit.*)

Fig. 37. Lemur mongoz (embryo). Hair-tracts of the upper limb. (From Schwalbe, *op. cit.*)

Epidermic scales (possibly significant of a reptilian ancestry) are said by Reh (*Jenaische Zeitschrift*, 1895, p. 190) to occur on the palmar and plantar surfaces of the extremities, and also on a remarkable callosity or pad near the wrist. This view (as to the significance of the scales) is not shared by Klaatsch (Reh, *op. cit.* p. 188) and Weber (*Die Säugethiere*, 1904, p. 29) presumably considers the analogy incorrect.

The nails (if the claw on the second toe be excepted) are flat, this character being especially remarkable in the nail of the hallux (or great toe). The ends of the nails are usually truncated in a very definite way: in some cases the margin tapers to a point, in others it is crescentic but with the convexity of the curve directed towards the root of the nail.

D. The Hands and Feet. The skin of the palmar (volar) and plantar aspects is of a dull greyish tint in the specimens mentioned above (cf. C). The character of the exposed surfaces demands a somewhat detailed description. In preparing an account I have consulted the works of Kidd¹, Whipple², and above all the unrivalled researches of Schlaginhaufen³. My personal observations are given in the sequel. The surfaces in question are uneven, as in the majority of mammals. For the epidermis is raised in the form of pads ("Ballen" of German authors); and of these, five (at the finger tips) are "apical," four (situated at the interdigital clefts) are "interdigital," while there is a single ("hypothener proximal") pad nearer the wrist (Fig. 38). It appears that the Lemurine type thus presents all save one of the series held by Whipple to be characteristic of the mammalian chiridium. The missing, or thenar proximal pad may be continuous with the first interdigital elevation⁴.

In addition to the pads, small nodular elevations of the surface are abundant (Fig. 38).

¹ Kidd, *The Sense of Touch in Mammals and Birds*, 1907.

² Whipple, "The Mammalian Chiridium," etc. *Zeitschrift für Morphologie und Anthropologie*, Band VII. 1904.

³ Schlaginhaufen, (a) "Das Hautleisten System," etc. *Morphologisches Jahrbuch*, Band XXXIII. 1905. (b) "Zur Morphologie der Planta," etc. *Zeitschrift für Ethnologie*, 1906.

⁴ The scheme of the primitive pads seen in the foetus of Man is slightly more complex. Cf. Retzius and also Schlaginhaufen, 1905, p. 669.

On these pads and on the larger nodules the epidermis is further distinguished by the presence of papillary ridges. The

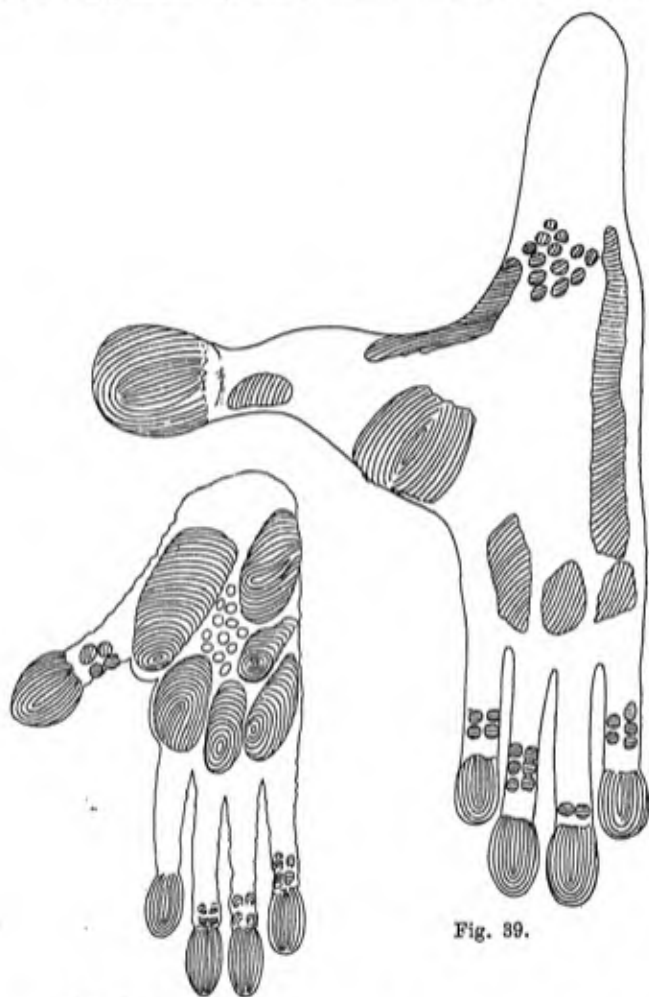


Fig. 38.

Fig. 39.

Fig. 38. *Lemur mongoz*. Papillary ridges of the hand. (Schematic. From a specimen in the Cambridge Anatomy School.)

Fig. 39. *Lemur mongoz*. Papillary ridges of the foot. (Schematic. From a specimen in the Cambridge Anatomy School.)

latter may be taken as indicative of the accession of a high degree of the tactile sense, and they confer this function on the various

eminences, which seem in their origin to have developed rather in relation to the rapid movements of a quadrupedal animal¹.

The papillary ridges in the Lemurs are said by Schlaginhaufen to arise through the coalescence of minute eminences at one period isolated from each other. Indeed a survey of the lemurine "planta" will suggest (Fig. 39) such an origin at once. But the "islands" thus described have a further definite character, since they themselves are marked by the orifices of several ducts (of sweat-glands) arranged more or less regularly in a circle. This feature, together with others of an histological nature, justifies their distinction as "insulae lenticulares" from another variety in which but one orifice and duct are present. The latter are called "insulae primariae" (Schlaginhaufen). It is noteworthy that the papillary ridges of the Lemurs are derived from such lenticular islands, whereas in the closely-allied Lorissinae (the so-called Slow-Lemurs) and in Man himself, the corresponding rôle is played by insulae primariae. The papillary ridges thus constituted traverse the several pads and also the larger nodules of the lemurine palm and sole. There they give rise to certain patterns (*figurae tactiles*) (Figs. 38 and 39), which may now be described briefly.

On the vola (palm), the ridges tend to the production of the appearances of concentric circles or inosculating loops. These are arranged on the proximal and interdigital pads, and in the centre of the vola the lines tend to run transversely across the long axis of the hand. The finger tips or apical pads are marked by loops (*sinus primarii*) which are widely open (*long lineae communicantes*). They enclose many longitudinal ridges (*fasciculi centrales*) and are found on the digital apex and even on the dorsal aspect as far as the edge of the nail.

The skin over the phalanges is nodulated and irregular. A few paired nodules bearing papillary ridges are seen here on each finger save the second. The ridges converge distally to the axial line of the digit.

On the planta (sole of the foot) the papillary ridges on the

¹ This view, viz. that the prime value of papillary ridges resides in their employment as sense-organs of touch, does not necessarily exclude the more mechanical influence they may possess, in rendering foot-hold or hand-hold more firm and less likely to slip.

proximal and interdigital pads appear as divergent and spirally curved lines. These are however related in a definite way, as shewn in Fig. 40 where the scheme of a series of loops (closed distally) is revealed. The presence of four *tri-radial* (Fig. 40, T_1-T_4) should be noticed. The loops are of course interrupted by the nodular character of the central portions of the planta, but on these

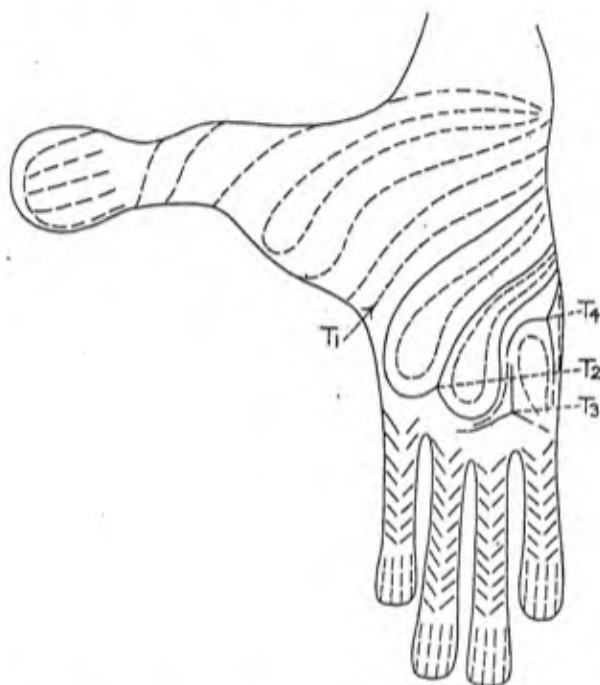


Fig. 40. Scheme of the papillary ridges of the foot of a Lemur. (After Schlaginhaufen, *op. cit.*) T_1-T_4 are the tri-radial mentioned in the text.

nodules lines in the appropriate direction can be detected with a lens. The apical pads are marked similarly to those of the hand, but that of the hallux is unusually large, and it is only here that the summits of the loops (sinus) are seen strictly on the plantar aspect. The phalangeal aspects bear nodules, and some of these are grooved in the case of each digit save the first; thus a slight difference is noticed between the hand and the foot.

A general survey of the palmar and plantar surfaces leads to the conclusion that the Lemurs represent a stage in the evolution of a more highly-developed type. In the latter the surfaces in question are more completely covered by epidermis marked with continuous *figurae tactiles*. Yet the Lemurs themselves are relatively elevated in comparison with most of the Eutherian mammals other than the Primates. We may regard the extent and moulding of the surfaces thus modified as indices of progressive specialization in the employment and interpretation of tactile stimuli. The psychological significance of these morphological characters is thus seen to enhance their value in elucidating the biological relations of the several representatives of the Primates in which they are here described.

E. The Skeleton. The skull (Fig. 41) is elongated, the brain-case being somewhat flattened, and the facial bones project as

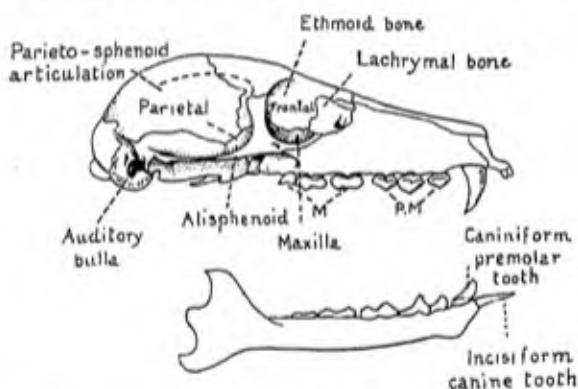


Fig. 41. Cranium, with mandible, of *Lemur varius*; note the auditory bulla, the articulation of parietal and alisphenoid bones, the facial extension of the lachrymal bone (cf. Fig. 21), the articulation of the frontal bone and maxilla behind the lachrymal bone, the small forward projection of the orbital plate of the ethmoid bone, the number of teeth, the small size of the upper and the great projection of the lower incisor teeth. In the mandible, the canine-like tooth is a pre-molar by position, and the canine tooth is incisiform.

a snout, at the extremity of which is the aperture of the nose. On the inner orbital wall, the frontal and maxillary bones join along a suture for a distance of about 5 mm., and thus widely separate the ethmoid from the lachrymal bone. The infraorbital nerve is provided with a groove not covered in to form a canal.

In the temporal fossa the alisphenoid joins the parietal bone, and thus the frontal and temporal bones are separated.

On the inferior aspect of the skull, the palate is seen to be much elongated: the glenoid fossa is so shallow as hardly to merit that description: there is a well-developed post-glenoid tubercle, and immediately behind this, a large foramen transmits the primitive jugular vein from the endocranial cavity. The external auditory meatus is shallow; it is formed by an "entotympanic" element¹ expanded in the form of a bulla, enclosing the tympanic ring: the latter may be overlooked unless carefully sought. The entrance to the carotid canal is in the posterior wall of the auditory bulla, close to the medial side of the stylo-mastoid foramen.

The sutures between the pre- and post-sphenoids, and between the latter and the basi-occipital bone as well as the metopic (interfrontal) suture, persist in adult life.

Most of the foregoing characters may be regarded as exemplifying conditions of the kind termed "primitive"; upon such details of evidence the decision as to the position of the Lemurs must finally rest. On the other hand, the presence of a post-orbital bar (between the orbital cavity and the temporal fossa) marks an advance on conditions otherwise primitive. Again, the position of the entrance orifice of the nasal duct on the facial surface (outside the orbit) might appear to be a lowly character: yet it is regarded by some (ex. gr. Forsyth Major) as a condition of specialization, determined by the enlargement of the orbital cavity and lachrymal bone, in relation to nocturnal habits.

The upper median incisor teeth are separated by a wide interval, and are two in number in each jaw on each side of the skull. On each side (above and below) is one canine tooth. The lower canine is so modified as to resemble an incisor, and the first lower premolar resembles a canine tooth. The position of the latter with regard to the upper canine tooth shews however that it is really a premolar, for it is posterior to the upper canine, whereas the true lower canine always comes in front of the upper

¹ Cf. Forsyth Major, *Proc. Zool. Soc.* 1899, and Kampen, *Morph. Jahrb.* 1905.

tooth of that name when the jaw is closed. (This view is not universally adopted: see Forsyth Major, *Geological Magazine*, 1900.) There are three premolar and three molar teeth; of the latter, those in the upper jaw bear usually three cusps (though two subsidiary cusps are often developed from the cingulum), and consequently suggest the tri-tubercular type. (For fuller details, cf. Chapter VI.)

Vertebral Column. The vertebrae usually number fifty-six, viz. cervical 7, thoracic 12, lumbar 7, sacral 3, caudal 27. The spinous process of the second cervical vertebra is very large; it quite overshadows the other cervical spines, and offers some resemblance to the corresponding part in the Dog.

Other resemblances to the same type of mammal may be observed in the thoracic region, where the tenth vertebra of that series is "anticlinal" (as in some Dogs); in the lumbar region, viz. in the number of vertebrae (7); in the presence of "anapophyses" (found also in the Cercopithecidae); and lastly in the curvature of the vertebral column as a whole. Such features may be termed "primitive"; probably they own a direct relation to the quadrupedal mode of locomotion: judging from the highest Apes and Man, they seem to be incompatible with the complete attainment of the erect attitude.

The sternum is rod-like, consisting of five large "sternebrae" in series, and one small ossified element between these and the elongated metasternal portion: eight rib-cartilages articulate with the sternum on each side.

The clavicle is relatively large and indicates the characteristic freedom of the upper limbs. The scapula is obliquely elongated and its coracoid process is slender, but falciform.

The humerus has a straight shaft, the outer lip of the bicipital groove being very prominent (probably the deltoid eminence is fused with it), while the inner lip is absent. At the lower end of the bone, the lateral supracondylar ridge is very prominent, the radial and coronoid fossae are clearly demarcated (as in Man) and an entepicondylar foramen is present.

The olecranon process of the ulna is relatively slender: at the lower end of the same bone, there appears to be an ossicle

(? ossiculum Vesalii) above the pisiform carpal bone, as in Hylobates.

In the carpus the os centrale retains its original independence: of the remaining bones, the metacarpals and proximal phalanges are of equal length, the intermediate phalanges almost equal to them, while the terminal phalanges are very short. The form of the phalanges is of importance in regard to the ancestry of the Lemurs. It is urged against the view that they are derived from the Condylarthra (cf. Earle, *Natural Science*, May, 1897).

The ossa innominata are elongated antero-posteriorly, i.e. in the opposite direction to that in which their characteristic width is shewn in Man. The iliac bones are long and narrow: the pelvic brim (true pelvis) is nearly circular, thus contrasting with many lower mammalian forms and approximating to the human type. The symphysis barely extends beyond the pubic bones, and the tubera ischii are smaller and less everted than in the lower Anthropeidea. The thyroid foramen is of great size.

The femur has a slender rectilinear shaft¹, a small globular head, and a short stout neck; a third trochanter may occur. At this level the shaft is "platymeric" with antero-posterior flattening, while at its lower end, the bone appears as though transversely compressed, when compared with the human femur. The patella is also narrow, but the general conformation of the knee-joint suggests a wide range of movement. There is a sesamoid bone, which often remains attached to the femur, in the outer head of the gastrocnemius muscle. The tibia is strongly platycnemic², and at the ankle the tibial malleolus is more elongated and larger than that on the fibula. The tarsus is flat, and the heel (os calcis) is prominent; the os calcis is elongated in some varieties (ex. gr. Galago) but not in Lemur (cf. *infra* Tarsius). The first metatarsal bone bears so large a tubercle

¹ In the giant extinct Lemurs known as *Megaladapis madagascariensis* and *M. insignis*, there is a curious flattening of the shaft, seen in both the humerus and femur, as though pressure had been applied in the sagittal direction. The specimens in the collections at S. Kensington and Vienna present these characters.

² The tibial flattening to which this appearance is due, appears most markedly in Lemurs, such as Galago, which have adopted a saltatory mode of progression. This has been pointed out by M. Vallois in an admirable memoir (*Bull. de la Soc. d'Anth. de Paris*, 1912, 3—4, p. 281).

for the *M. peroneus longus* as to suggest that this muscle acts here as an adductor of the hallux, thus strengthening the grasping power of the foot. The hallux is long, and distinctly stouter than the other digits. The terminal phalanges of all the digits are very small in comparison with those situated more proximally: the terminal phalanx of the second digit is tapering and spine-like, and thus corresponds to the peculiar shape of nail which it bears.

F. Muscular System¹. 1. The subcutaneous musculature. This system of muscles is well developed about the head and neck, as shewn in the accompanying sketch of a dissection (Fig. 42).

Several divisions of the facial musculature can be recognized; and below the mandible, the cutaneous musculature is divisible into a superficial (*platysma*) stratum and a deeper sheet corresponding to the *M. sphincter colli* (cf. Ruge, quoted by Wiedersheim: *Structure of Man*, p. 106), Fig. 42.

The dorso-humeral sheet is also well developed.

2. Of the submental muscles, the digastric is perhaps the most noteworthy. In appearance it resembles the corresponding muscle in some of the Marsupialia (*Macropus*). The distinction of an anterior and a posterior belly is barely perceptible. A continuous muscular band extends from the occipital bone forwards, to be attached to the deep surface of the body of the mandible just in front of the foremost fibres of the masseter muscle (the latter curves inwards round the lower margin of the jaw). The stylohyoid muscle crosses the digastric superficially. Near this place, the digastric has a tendinous strip

¹ The muscles are grouped in eight divisions bearing certain relations to the functional characteristics and adaptations of the animal. These divisions are defined briefly as follows:

1. The cutaneous musculature, especially the "muscles of expression."
2. The submental muscles, especially the *M. digastricus*.
3. Muscles used in balancing the head or in moving that part.
4. Musculature of the shoulder, as related to arboreal life and the corresponding mode of progression.
5. Muscles of the arm and forearm in relation to prehension.
6. Muscles of the digits of the hand.
7. The diaphragm.
8. Muscles of the pelvis and lower limb, in relation to the erect attitude.

along its upper margin. A tendinous strand is seen among the fibres of insertion¹.

3. The sternomastoid muscle has thin ribbon-like sternal and clavicular heads. These stand in contrast to their massive counterparts in Man, and seem to subserve another function, probably in relation to the difference in attitude. The XIth cranial nerve pierces the muscle, which is a wide sheet near its occipital insertion. It blends with the *M. trapezius*, and even

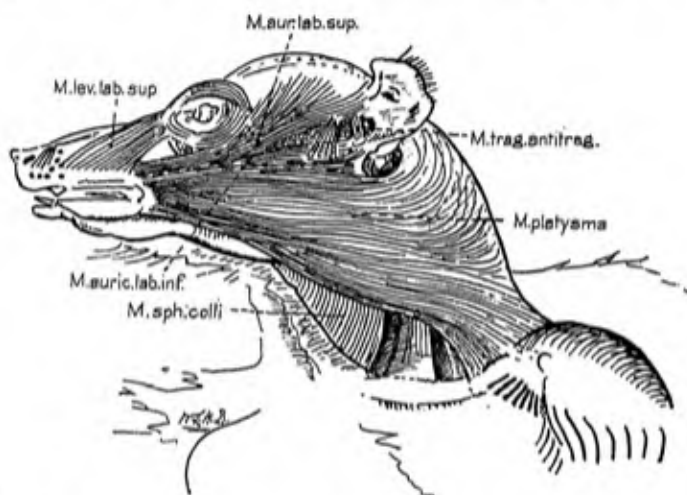


Fig. 42. Cutaneous musculature of the head of *Lemur mongoz* to shew some of the more definite constituents of the muscular sheet. (From a specimen in the Cambridge Anatomy School.)

encroaches on the ligamentum nuchae. The *M. trapezius* thus fails to obtain an attachment to the occiput, unless this be represented by the occipito-scapular slip of muscle seen on the surface of the *M. trapezius*. The latter is reinforced by an extensive "rhomboid" sheet on its deep aspect.

4. The shoulder-muscles include the powerful *M. deltoideus*, which arises from the whole length of the scapular spine (lower margin), and at its insertion shares the external lip of the bicipital groove with the *M. pectoralis major*. The latter muscle has no

¹ For the form of the *M. digastricus* in *Macropus*, etc., cf. Toldt, *Sitz. der k. k. Akad. der Wissen. zu Wien*, Band cxvii. Abt. iii. Math. Nat. Kl. 1908.

"clavicular" component. The *M. pectoralis minor* is attached partly to the aponeurosis of the *M. obliquus externus abdominis*. Yet on the whole, suggestions are afforded to the effect that these shoulder-muscles are less highly developed than in the more purely arboreal Simiidae.

The *M. latissimus dorsi* has no scapular area of origin: nor does it blend with the *M. teres major*.

The *M. dorsi-epitrochlearis* arises, not from the tendon of the *M. latissimus dorsi*, but by two "heads," one from each aspect of the fascial sheath of that muscle. The heads blend to form a muscle traceable below to the olecranon, and thence forwards to the deep fascia over the internal epicondyle and forearm.

5. The *M. biceps brachii* is provided with a *lacertus fibrosus* of remarkable form, for a bundle of muscular fibres leaves the muscular part of the *M. biceps* to be inserted into the fascia over the *M. pronator radii teres*. The *M. coraco-brachialis* is double, part passing dorsally to the tendon of the *M. latissimus dorsi* to be attached to the humeral shaft in that region. The remaining part represents the muscle as seen in Man save that it extends nearly to the internal epicondyle of the humerus. This muscle appears therefore as a more important element in the arm of the Lemur.

6. In the forearm, the *M. flexor longus pollicis* is in the primitive condition of union with the deep flexor muscle of the other digits. Moreover it receives a large contribution from the more superficial part of the *M. flexor sublimis digitorum*, and thus from the internal epicondyle of the humerus.

The pollex is furnished with two extensor muscles, viz. for the metacarpal bone (*M. abductor longus*), and for the terminal phalanx, the *M. extensor pollicis brevis* being undeveloped. The annular ligaments at the wrist seem to be very strong in comparison with these structures in Man.

7. The Diaphragm is a thin sheet where it arises from the ribs, and its crura are rather more distinct from the costal portion than in Man. This contrast may well be explained in the light thrown on the relation of the Diaphragm to the habitual attitude and the mode of life of the animal (cf. Dr Wood-Jones, *J. A. P.*, April, 1913).

8. The muscles of the lower limb attract particular notice on account of the modifications induced in their human representatives owing to the assumption of the erect attitude.

In the Lemur, the *M. gluteus maximus* appears definitely as a sheet arising from (a) the posterior superior spine of the ilium, (b) the fascia over the back and lower end of the sacrum, (c) an aponeurosis over the caudal vertebrae, and (d) from the transverse processes of two caudal vertebrae, this (d) being the thickest part. It is inserted into the femoral shaft. Though extensive in origin, the muscle is nevertheless a mere sheet. Anteriorly to it, a second sheet-like muscle arises from the iliac crest as far as the anterior superior spine and is attached close to the *M. gluteus maximus* on the femur. This may well represent the original form of the human *M. tensor fasciae femoris*.

The *M. biceps femoris* has no "short" or femoral head. It arises (with the *M. semitendinosus*) from the tuber ischii, and is inserted, not into the fibula, but into the fascia of the leg, some of its fibres being traceable almost as far as the external (fibular) malleolus at the ankle. The *M. tenuissimus*, representative (in certain mammals) of the short head of the *M. biceps*, has not been recognized in the Lemurs¹.

The *M. adductor "brevis"* is longer and larger than the *M. adductor "longus."* The *M. gracilis* blends below with the cord-like *M. semitendinosus* (as in *Tarsius*, *v. infra*).

A curious muscular strip winds spirally round the capsule of the hip-joint. In position, it corresponds to the lower limb of the human ilio-femoral ligamentous band.

The chief features of the *M. quadriceps extensor cruris* are (1) the enormous size of the *M. vastus lateralis* (which runs up to the trochanter anteriorly as well as laterally), and (2) the connecting slip between this muscle and the *M. rectus femoris*. These conditions are encountered again in *Tarsius* (*v. infra*).

Of the muscles below the knee-joint, we may note that the *M. tibialis anticus* is of very great size, and that the *M. tibialis posticus* has no tibial attachment (*v. infra* *Platynemia*). In this respect it resembles the *M. soleus* which likewise contains no tibial fibres, and in this respect presents the primitive form

¹ Cf. Klaatsch, *Morphologisches Jahrbuch*, Band xxix. 1902, p. 263.

of this muscle. The *M. plantaris* is large and distinct. Its tendon is remarkable for extending beneath and beyond the os calcis, where it widens out as the plantar fascia. The latter structure and the adjacent muscles of the foot are so important as illustrations of the arrangements in the prehensile form of that organ, that a somewhat detailed description seems admissible (Fig. 43).

(i) The plantar fascia, directly continuous as already stated with the tendon of the *M. plantaris*, becomes wider as it is traced distally, and then gives off the distinct aponeurotic band to the hallux (as described by Loth, *Korrespondenzblatt der Deutschen Anthropologischen Gesellschaft*, XXXVIII. 1907), and finally contributes feebler offshoots to the remaining digits. The *M. abductor hallucis* receives some muscle fibres from its tibial margin and "deep" aspect. The *M. abductor minimi digiti*, arising from the os calcis, contributes a muscular fasciculus to the same "deep" aspect of the plantar fascia. The narrowness of the fascia and its strong offshoot to the hallux are considered to stand in direct relation to the predominantly prehensile function of the foot (Loth).

(ii) The *M. flexor brevis digitorum pedis* arises in two ways, viz.

(a) From the deep aspect of the fascia plantaris: this portion sends a "perforated" tendon to the *second* digit.

(b) The second and chief origin is taken from the tendon of the *M. flexor digitorum longus* (or *flexor tibialis*). This part contributes the perforated tendons to the third, fourth and fifth digits. Nerve fibres come from the medial plantar nerve-trunk, though in some instances the lateral plantar nerve sends fibres to the slip to the fifth digit¹.

(The hallux or first digit has thus no perforated tendon: nevertheless a superficial though not a perforated tendon runs to it from the tendon of the *M. flexor digitorum longus*.)

(iii) The *M. flexor digitorum longus* has a tendon more slender than that of the *M. flexor hallucis longus* (but stouter than the tendon of the *M. tibialis posticus*). This tendon gives offshoots to all five digits, and these offshoots (with the exception of that to the hallux) perforate the tendons provided by the *M. flexor brevis*

¹ Sawalischin, *Morph. Jahrbuch*, Band XLII.

as described in (ii) above. The tendon to the hallux is not perforated, but it accompanies the tendon of the *M. flexor hallucis longus*. The *Mm. lubricales* are not primarily associated with the *M. flexor tibialis* (*flexor digitorum longus*).

(iv) The *M. flexor hallucis longus* (*flexor fibularis*) arises from the tibia as well as from the fibula, and terminates in a tendon of great strength which passes through a tunnel beneath the entocuneiform bone. Beyond this the tendon divides into five slips for the digits. That to the hallux receives the slender tendon from the *M. flexor digitorum longus*. The other four slips provide the *lumbrical* muscles, and are also joined by the tendons of the *M. flexor digitorum longus* (*tibialis*). Each deep tendon is thus really double, and the distinction is readily to be ascertained. Moreover in the first and fifth digits, the tendon derived from the *M. flexor digitorum longus* (*tibialis*) winds round that derived from the *M. flexor hallucis longus* (*fibularis*)¹.

A review of these complicated arrangements or a comparison with those in the human hand and foot respectively, leads to the inference that the determining factor is probably the necessity for providing a strong grasp. The same conclusion will be drawn from the general form of the foot, particularly perhaps in regard to the wide angle of separation of the hallux from the remaining digits. The interosseous muscles are (as in the human *hand*) disposed with reference to an axis passing through the median digit.

On the whole, it appears that the musculature of the Lemur differs from that of Man not so much in regard to the identity of individual muscles, as in their disposition and attachments. These differences are largely determined by the attitude habitually adopted in each case.

G. Vascular System. The heart² is conical, having transverse and dorsi-ventral diameters of nearly equal length. In formalin-hardened specimens the acute and obtuse margins are distinct. Both ventricles extend to the apex of the heart. The long axis of this organ is sharply inclined to the axis of the post-caval vein

¹ For variations in the Lemur and other Primates, the excellent paper by Sawalischin in the *Morphologisches Jahrbuch*, Band XLII. Heft 4, 1911, should be consulted.

² Patten, *Trans. Roy. Acad. Medicine in Ireland*, Vol. XVII. 1899.

and the pericardium is comparatively limited in its attachment to the diaphragm. The aortic arch gives off two vessels, one being the innominate artery whence the right subclavian and both common carotid arteries arise. The remaining vessel is the left

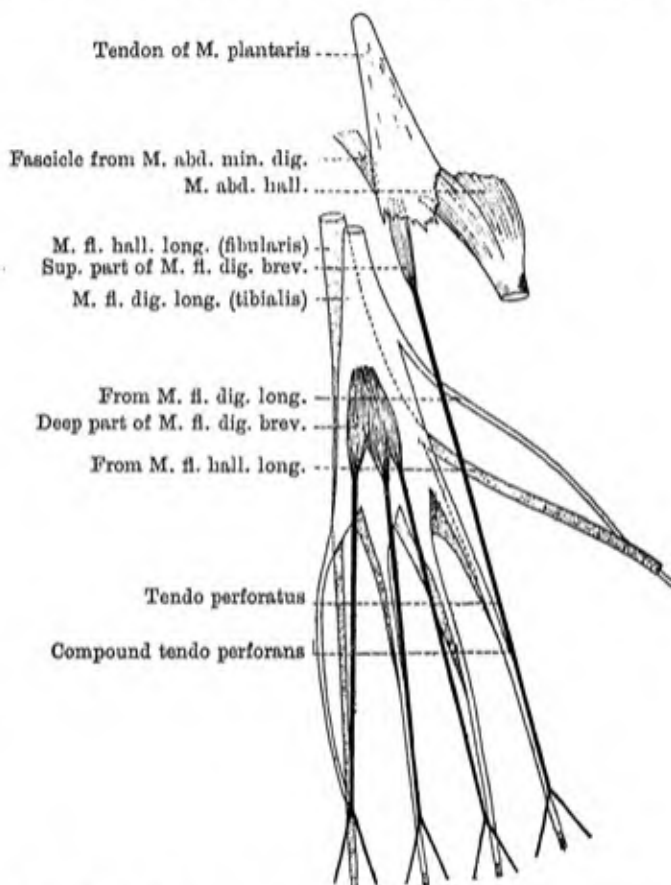


Fig. 43. Lemur mongoz. Scheme of the flexor tendons of the toes. (Mus. Anat. Cant. From a dissection. W. L. H. D.).

subclavian. The pre-caval vein like the trunks just mentioned is relatively elongated. The post-caval vein is exposed within the thorax for a short distance in its whole circumference, and lies in relation with the subpericardial pleural sinus and the contained lobus impar of the right lung.

All the foregoing characters are primitive, and correlated with the narrowness of the proximal portion of the thoracic cavity.

The position of the carotid foramen and the direction of the carotid canal in the skull shew that in Lemurs as in the lower Apes, the artery enters the skull obliquely, *i.e.* with an angle widely open to the ventral aspect. The entrance to the carotid canal is close to the medial side of the foramen stylo-mastoideum. Winge describes the internal carotid artery as dividing in its course through the canal, or rather as giving off a stapedia branch from which the middle meningeal artery is ultimately derived.

In the Lemurs of the family Lorissinae, the brachial and femoral arteries divide suddenly into many parallel minute branches constituting a form of "rete mirabile." The explanation of this remarkable condition (apparently subversive of the expectations based on morphological principles) has yet to be provided. That the basis is physiological can scarcely be in doubt. Moreover the Lorissinae have a curious reptilian slowness of movement. Yet the presence of similar arterial subdivisions in the limbs of the essentially active Tarsius (as described by Burmeister, *v. infra*, p. 111), shews that the explanation must be sought in some other connection.

The axillary artery is characterized by a tendency to the development of a subscapular offshoot whence four vessels arise, *viz.* the Aa. circumflexa humeri, circumflexa scapulae, thoraco-dorsalis and subscapularis. The brachial vessel is of the "superficial" type (*i.e.* it passes downwards superficially to the median nerve) and it sends an offshoot to pass with the median nerve through the entepicondylar foramen. In the Lemuroidea, first among the lower quadrupedal mammals, the ulnar artery begins to assert itself as a contributor to the palmar arterial arches.

In the lower limb, the common femoral trunk often gives off the A. circumflexa lateralis. An A. saphena, of the type so distinctive of the higher Primates, is not usual. In the foot, the medial plantar artery is of large size and extensive distribution. The lateral plantar artery is not found.

H. **Nervous System: the Brain** (Figs. 44, 45). Some of the cerebral characters of the Lemuroidea have been enumerated already (cf. p. 46). They were adduced in support of the case for the inclusion of the Lemurs in the Order Primates. Here it is necessary to add further details. But in setting out these features, and in any attempt to appraise their value in evidence, certain preliminary considerations must be borne in mind.

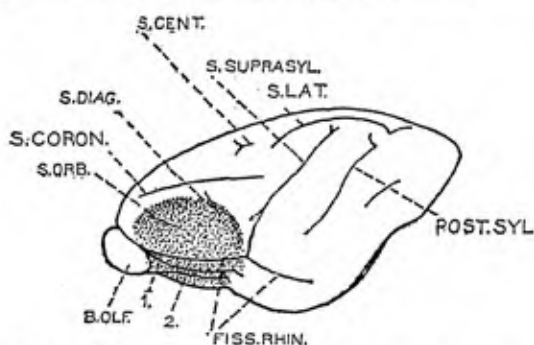


Fig. 44. Brain of Lemur mongoz. Lateral aspect. (Mus. Anat. Cant.)

(i) Some features of the Lemurine brain are undoubtedly primitive as compared with the corresponding characters in the animals grouped together as the Sub-order Anthropoidea. Of such characters, the most impressive example is probably that afforded by the conspicuous olfactory bulb and tract.

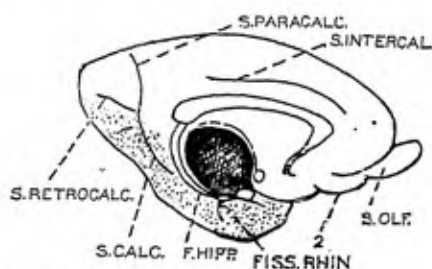


Fig. 45. Brain of Lemur mongoz. Mesial aspect. (Mus. Anat. Cant.)

(ii) Other characters, though seemingly primitive, may nevertheless indicate a reversion or a degeneration: the relatively feeble development of cortical folding in the "true" Lemurs may be cited as an example of characters determined by such processes.

(iii) Again, the possibility of special adaptations has to be taken into account. Having regard to the nocturnal habits of many Lemurs, the student must be prepared to recognize (and possibly to discount) exuberant development of the parts directly connected with vision and hearing.

(iv) In such investigations, the absolute size of the animal is a factor of importance. For instance, large animals will be found to possess (*ceteris paribus*) a higher grade of cortical folding or complexity than smaller forms.

These considerations will be discussed more fully in a later chapter, but they demand prominence in any comparison of brains.

With such introductory principles in mind, we may now consider the brain of the Lemur as described in the following paragraphs.

(a) Rhinencephalon¹. The olfactory bulbs (Figs. 44 and 45) are of relatively large size and sessile, *i.e.* in close contact with the brain. The rhinencephalon is separated from the neopallium by a rhinal fissure which varies as regards its distinctness in particular species.

(b) The marginal pallium is limited by a hippocampal fissure, which is nearly vertical in direction. The uncus, hippocampus major, the sub-splenic gyrus A. Retzii, the fimbria and fornix are all distinct.

(c) The neopallium is (comparatively) feebly convoluted, and the true Sylvian fissure is present, though only the hindmost part of this fissure, as seen in the higher Primates, is present in the Lemur's brain. The illustrations (Figs. 44, 45) may be consulted for the other sulci.

(d) In contrast with the conditions obtaining in the higher Primates, the occipital lobe in the Lemurs is usually small, and it therefore fails to overlap much of the cerebellum. The posterior cornu of the lateral ventricle is not present.

(e) The motor and visual areas of the cortex are extensive. Here we may add that the frontal, temporal and parietal association areas are relatively limited in extent. The distribution of these cortical areas on the neopallium is shewn in Figs. 46 and 47².

"Limiting" sulci or fissures are represented in these figures by the fissura rhinalis.

¹ These terms are defined in a subsequent chapter. The descriptions are based upon the publications of Professor Elliot Smith mentioned in the footnote on p. 43.

² The areas shewn in these charts are those given by Dr Brodmann (*Vergleich. Lokalisationslehre der Grosshirnrinde*, 1909). They differ in position and extent from those described by Dr Mott (*cf. Collected Papers from the Pathological Laboratory of the London County Asylums*, 1909, p. 490).

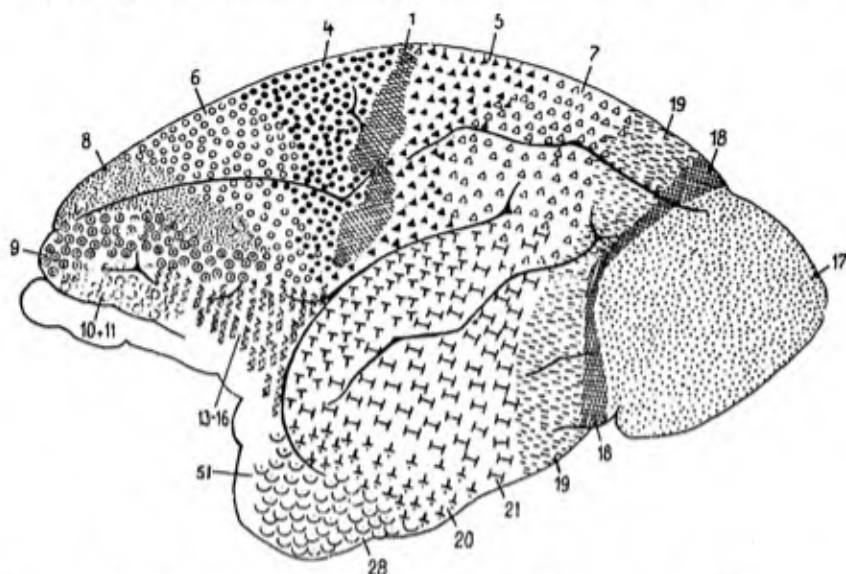


Fig. 46. Cortical areas in the brain of a Lemur. (From Brodmann, *op. cit.*)

No. 1. Area post-centralis ("sensory").

No. 4. Area giganto-pyramidalis ("motor").

No. 17. Area striata ("visual").

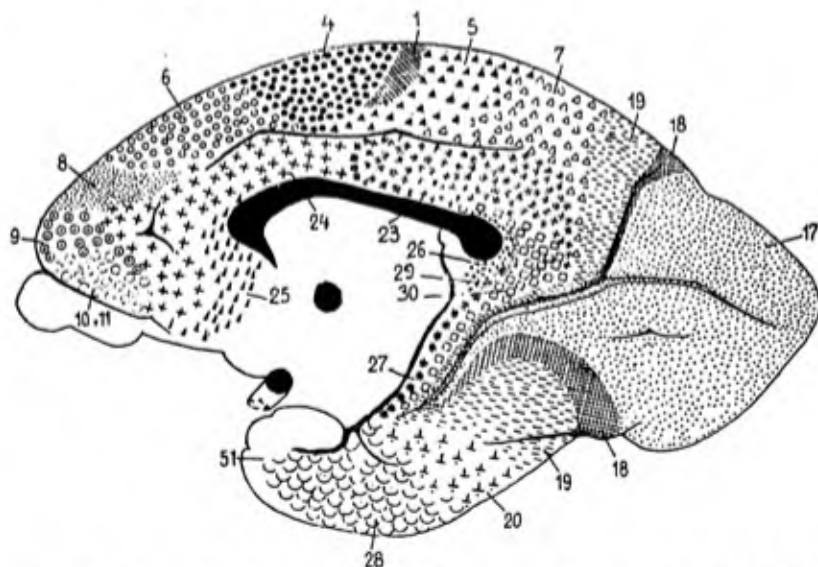


Fig. 47. Cortical areas in the brain of a Lemur. (From Brodmann, *op. cit.*) Mesial aspect of hemisphere. References to areas Nos. 1, 4, and 17 are given under Fig. 46.

(f) The optic thalami are of unusually large dimensions in the brain of the Lemur, and this development suggests high specialization of the visual sense.

(g) Judged by the appearance of the mesial sagittal section, the cerebellum in the Lemurs is more developed than that of the lower mammals, and approaches the form characteristic of the apes. But the lateral expansion (probably in relation with the relatively small neopallium) is distinctly less than in the higher Primates.

The peripheral nervous system cannot be described here in detail. My observations on *Galago garnetti* confirm those of Bolk¹ showing that the brachial plexus is of the "post-fixed" type², as contrasted with at least one frequent human type of plexus. (Cf. p. 143.)

I. Respiratory System: the Larynx. The ventricles are not prolonged into the extensive sacculi so distinctive of some of the higher Primates. In some Lemurs (ex. gr. *Galago garnetti*: cf. Fig. 48) unusually large and isolated muscle-fibres are seen in coronal sections of the larynx. These fibres are adjacent to the *M. thyro-arytenoideus* (external part).

The Trachea. This is distinguished by the fact that the cartilaginous rings are complete (in Lemur), though weaker behind, where the cartilage is discontinuous in other forms.

The Lungs. The left lung has three lobes, the middle of these passing into a long falciform process in front. Both the aorta and the oesophagus groove this lung³. The right lung has (in addition to the three lobes found in Man) a lobus impar which is insinuated between the oesophagus behind and the post-caval vein (inferior vena cava) in front. It extends thus beneath the pericardial sac, being enclosed in a diverticulum (the sinus subpericardiacus)⁴.

The pleural sacs converge behind the sternum to meet at the level of the third costo-sternal joint. Thence distally they

¹ *Der plexus cervico-brachialis der Primaten*, Petrus Camper, Di. 1. Af. 4.

² Cf. Wilfrid Harris, *J. A. P.* July, 1904.

³ Cf. Patten's description of the thoracic and abdominal viscera in the *Transactions of the Royal Academy of Medicine in Ireland*, Vol. xvii. 1899; also in *Proc. Anat. Soc.* 1900. Patten describes *Lemur varius*, while the notes above are based on an examination of *Lemur mongoz*.

⁴ Ruge, *Morphologisches Jahrbuch*, Band xviii.

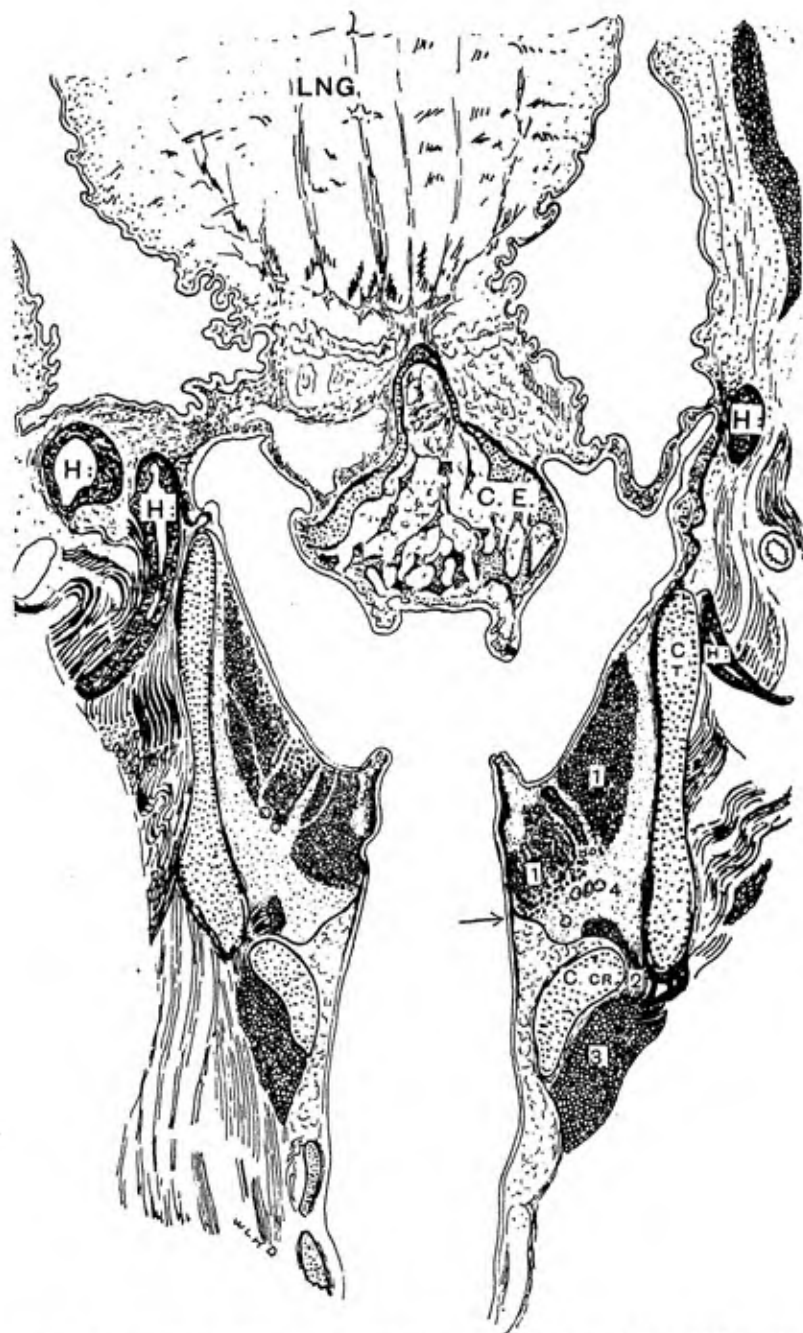


Fig. 48. *Galago garnetti*. Vertical coronal section through the middle part of the plica vocalis. 1, m. thyro-arytenoideus; 2, m. crico-arytenoideus lateralis; 3, m. crico-thyroideus; 4, large isolated muscular fibres. Large isolated muscle-fibres are seen to the outer side of the m. thyro-arytenoideus. The m. crico-thyroideus seems to be kept outside the thyroid cartilage owing to the overlap of this cartilage as regards the cricoid cartilage. ($\times 8.3$.)

remain in contact as far as the ensiform cartilage, and thus cover the pericardium completely below. Posteriorly the pleural sacs pass far down the vertebral column, extending in some cases to the level of the first lumbar vertebra¹.

J. The Alimentary Canal. The Lips. Vertical sections of these shew the bundles of the *M. orbicularis* cut across. The appearances resemble those of the lower Anthropoidea and present few features of distinction.

The Stomach is simple in form and is covered largely by the Liver.

The Liver fits like a cap or pallium over the stomach and adjacent organs. In common with these, it is situated more caudally than in the highest Primates, including Man (Patten). The following points have been selected for notice, as bearing upon the general morphological status of the Lemurs.

(a) In general, the liver conforms to a type which may be described as quadrupedal. A tendency to multi-lobation is one of the features of that type, but in the Lemurs this tendency is exaggerated (Ruge²) by the development of minor flange-like lobules.

(b) In its mode of fixation to the diaphragm and posterior abdominal wall, the liver of the Lemur conforms again to a primitive type. Thus the connexion is provided by peritoneal folds (the ligamentum falciforme and ligamentum coronarium), as in all the Primates. The falciform ligament and the left portion of the coronary ligament require no special description. But the right portion of the coronary ligament has a *linear* attachment, i.e. no separation of peritoneal laminae (leaving a "bare area" of contact between the liver and the diaphragm) exists. The possession of a wider area of contact is reserved for the highest of the Primates. It has been regarded as consequential on the assumption of the erect attitude³. This explanation is doubtless correct, although the "attitude" habitual in many Lemurs enjoins hesitation in its unqualified acceptance.

¹ Patten, *op. cit.* v. p. 88 *supra*.

² *Morphologisches Jahrbuch*, Band xxix., also xxx. and xxxv. "Die äusseren Formverhältnisse der Leber bei den Primaten."

³ *Proc. Anat. Soc.* 1899, February.

(c) The incisura oesophagea is very deep and of considerable extent in the cranio-caudal (antero-posterior) direction. In a Lemur mongoz dissected by me, it constitutes also an incisura gastrica. Such a deep incisure is again a mark of the primitive status of its possessor.

The liver has also characters distinguishing it from those of the higher Primates, though not necessarily primitive in themselves. Among such characters, the following are to be ranked.

(a') An enormous incisura duodenalis on the right side, in which the duodenum comes to the surface between the right central and right lateral hepatic lobes.

(b') The left lateral lobe curves forwards and extends across the mid-ventral line to the *right* hypochondrium.

(c') The lobus caudatus is divisible into a pars papillaris (lobus Spigelii of human anatomy) and a lobus caudatus proper. Of these, the papillary portion is insignificant and projects but slightly beyond its surroundings. The true caudate portion is on the contrary extensive. Passing downwards, it is hooked round the inner aspect and lower pole of the right kidney.

(d') The impressio renalis is consequently provided by the caudate lobe and the right lateral lobe conjointly.

The Pancreas is already much attenuated where it crosses the aorta on its way towards the left kidney (cf. Patten, *op. cit.*).

The large size of the duodenum is noteworthy. This part of the intestine consists of a longer vertical part, and a shorter transverse part, distal to the former; it crosses the vertebral column at a level as far back as that of the fourth lumbar vertebra. The caecum is prolonged into a tapering appendix of some size (Fig. 49).

The loop in the transverse colon has been mentioned in an earlier chapter. Here it will suffice to note that the loop is "sinistral" in the viscera (cf. Fig. 50) examined (*i.e.* from a specimen of Lemur mongoz). In Galago garnetti I find the loop is dextral, as it is said to be in Propithecus diadema¹, in which the loop is far more complicated than in Lemur mongoz, and is

¹ Cf. Max Weber, *Die Säugethiere*, 1904; also Beddard, *P. Z. S.* 1908, May 26, p. 578, and Mitchell, *Zool. Trans.* xvii. Part v. Dec. 1905 (for an account of the colic loop in other mammals).

quite comparable with the corresponding part in certain artiodactyle Ungulata. Whatever the determining factor may prove to be, and it is at present obscure, the condition is certainly not a primitive one; on the contrary, it probably indicates specialization in regard to diet.

The elongated rectum presents no features of particular importance.

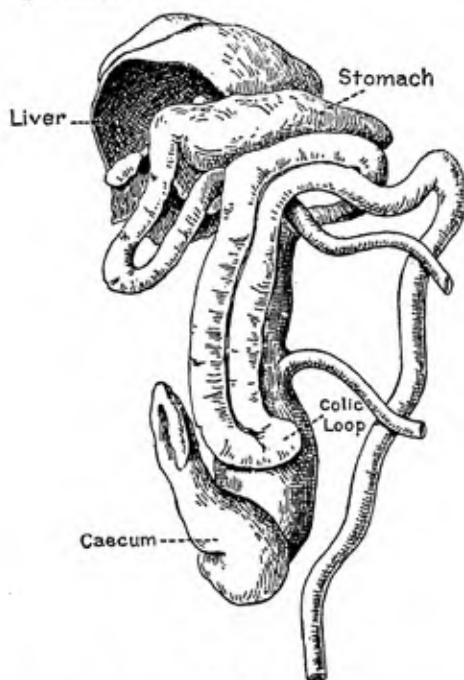


Fig. 49.

Fig. 49. Sketch of the viscera of *Lemur mongoz*. (Mus. Anat. Cant.)

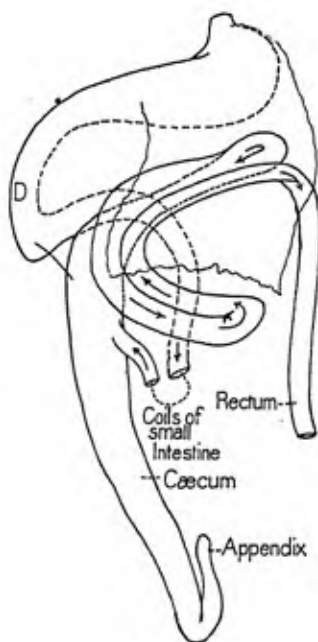


Fig. 50.

Fig. 50. Projection drawing of the same. D. Duodenum.

The Spleen is an elongated crescentic organ fitted round the lateral convex margin of the left kidney. In form, the spleen is said to resemble those of quadrupeds rather than those of the higher apes.

K. Urogenital System. The kidneys are placed asymmetrically, that on the left side being more caudal (distal) in position than that on the right side of the abdomen. Thus the relation is

exactly the converse of that obtaining in Man. The relation of the right kidney to the caudate lobe of the liver has been noted above. Beside the liver (and the adrenal body) the duodenum and colon touch the right kidney, the duodenum being placed further from the mid-line than the colon, and herein again the contrast with the human arrangement is striking. The testes¹ occupy a scrotum either alongside or just posterior to the root of the penis. The scrotal sac is provided with a "cremaster" muscle derived from the *M. transversalis abdominis*.

The penis contains a simple rod-like bone developed on the dorsal aspect of the urethra (by which it is not perforated as in some forms) in the free part of the organ. The free part of the penis is further characterized by an armature of thorn-like and horny excrescences, and of these three near the base of the penis are larger than the others and are directed proximally (analogous spines are described in the rodent *Dipus* or *Jerboa*).

A definite corpus spongiosum distinguishes the true Lemurian urethra from that of *Nycticebus*. In most of the above characters, the "true" Lemurs are the most primitive of all the Lemuroidea.

The bladder is of the primitive "tubular" form.

The sperm-cells² (Fig. 51) are distinguished by (a) the great length of the pars conjunctionis (*Verbindungsstück*) containing the centrosomes; (b) the great relative width of the nuclear portion of the head. Of these characters, the first is more constant than the second among the Lemuroidea.

In the female Lemur, the Fallopian tubes are short, though coiled: the clitoris is of very considerable size³.

II. TARSII.

The anatomical characters of *Tarsius* have led authorities of great distinction to regard it as the most primitive of all living Primates. Such an animal commands a very special interest. I think it desirable to remark that the possession of characters testifying to the conclusion formulated above, is quite compatible

¹ From the descriptions of Kaudern, *Zoologische Jahrbücher*, 1910.

² Retzius, *Biologische Untersuchungen*, N. F. Band xiv. 1909; also Band xvii. 1912.

³ Patten, *op. cit.*

with specialization in certain respects. In fact *Tarsius* really presents a very remarkable combination of features: in their description the same sequence will be adopted as for the *Lemur*.

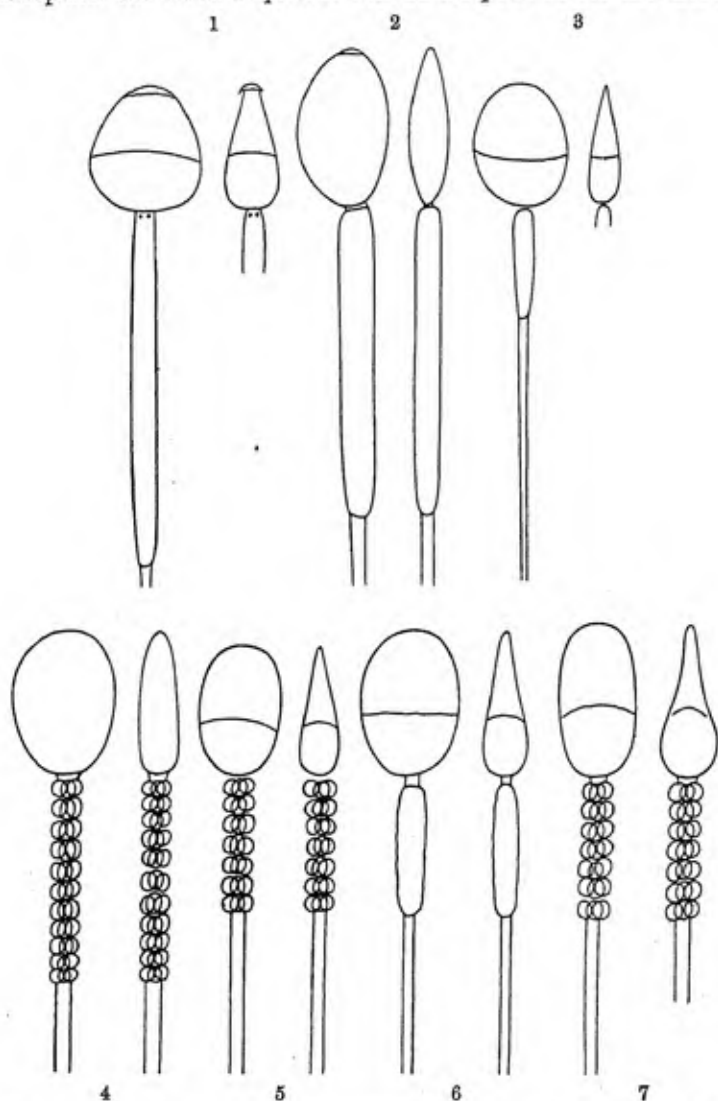


Fig. 51. Spermatozoa of various examples of the *Primates*. Two views (front and side) of each type are shewn, and all are very highly magnified. 1, *Lemur*. 2, *Macacus*. 3, *Hylobates*. 4, *Orang-utan*. 5, *Chimpanzee*. 6, *Man*. 7, *Gorilla*. (After Retzius.)

The literature on the anatomy of *Tarsius* is not scanty, but it is somewhat scattered. My descriptions are based principally on the examination of specimens in the Cambridge Collection: but I freely admit the guidance of such writers as Burmeister¹, and Professors Elliot Smith², Leche³, Ruge⁴, and Schlaginhaufen⁵.

A. External characters. The principal characters of *Tarsius* have been enumerated in an earlier chapter (p. 47). In revising the list so far as external appearance is concerned, the small size of the animal, and its disproportionately large eyes (Fig. 52), first claim attention. The face is short and flattened in contrast with those of Lemurs, and it is almost certain that the visual fields overlap so far as to provide "stereoscopic" vision. The curious manner in which the head is capable of rotation is shewn in the illustration. This bird-like habit was noted in the first description of a living *Tarsius*. Inspection of a mounted skeleton of *Tarsius* reveals little in the cervical vertebrae that is obviously suggestive of this faculty⁶; moreover it is not entirely unknown among human beings, though of course anomalous among these. Physiologically, it makes provision for a wide visual survey, and it is remarkable that movements of the head as a whole, rather than lateral movements of the eyeballs, should be conspicuous. Probably the inertia of the large eyes is involved in this. Food is seized with the fore-limbs and thus conveyed to the mouth (*Cheiromys*⁷ does the same, while the true Lemurs tend to seize food in their jaws, though the limbs may be employed as well).

Though of arboreal habits, *Tarsius* is none the less a saltatory animal. In a sense, indeed, *Tarsius* may be said to have acquired the erect attitude; certainly it has adopted a bipedal mode of locomotion. In its leaps, *Tarsius* strangely resembles a Frog, and

¹ Burmeister, *Beschreibung der Gattung Tarsius*, 1846. This monograph is of classical value: the descriptions are admirable, and the author's illustrations are noteworthy both for their accuracy and their high artistic value.

² *Linnaean Transactions*, Vol. VIII. Part 10, 1903. Presidential Address, Section H, British Association, 1912.

³ Leche, *Klassen und Ordnungen*, Lieferungen 54—56, 1899.

⁴ Ruge, *Morphologisches Jahrbuch*, Band xxix. 1902.

⁵ Schlaginhaufen, *Morphologisches Jahrbuch*, Band xxxii. 1905.

⁶ *v. infra* however for peculiar characters of these vertebrae.

⁷ *Auctore*, Professor Elliot Smith.



Fig. 52. *Tarsius spectrum*, a representative of the Sub-order Tarsii (the figure is slightly less than the life-size of the animal).

as in that Amphibian, the anatomical conformation of the hind limbs is greatly specialized. This is most marked perhaps in the muscles of the thigh. Again in the proportions of the respective toes, a close resemblance obtains between *Tarsius* and the arboreal frog *Phyllomedusa*. Abel¹ has admirably discussed the significance of the elongated tarsal bones (to which *Tarsius* owes its scientific name) and has pointed out the morphological differences between *Tarsius* and other saltatory mammals (ex. gr. *Macropus*). It will suffice to note here that *Tarsius* has acquired the requisite modifications and proportions of the hind-limbs without sacrificing the prehensile function of the foot, and it is still to some extent plantigrade. (In the Frog, the provision for swimming had to be safeguarded.) In most saltatory mammals such functions have been waived, and the necessary elongation is provided through the metatarsal bones rather than the tarsus. Among the Lemurs certain forms, ex.gr. the Galagos, are also saltatory, and in these the changes, which have reached their climax in *Tarsius*, are seen in a less advanced stage.

The tail of *Tarsius* is long and (in some cases at least) it is provided with a terminal tuft recalling that of the *Jerboa* (*Dipus*). The tail probably fulfils an important function in preserving equipoise during the rapid movements of the animal, and I think that the presence of a cutaneous patch (with grooves) found on the ventral aspect, suggests some development of a prehensile function also.

Yet another striking peculiarity is seen in the curious spatulate digits: these are irresistibly reminiscent of the corresponding parts in the Gecko, though in detail very different.

B. The Hair². (1) As in Lemur, the "sinus" hairs or vibrissae will be considered first. They include three main groups, viz. the supra-orbital, naso-labial, and malar or cheek series, but the pigmented pads (from which the hairs project in Lemurs) are either absent or indistinct. The vibrissae at the wrist of the Lemur are not recognized by Schwalbe, save in the form of a transient embryonic elevation on the part concerned. The eye-lashes arise from the surface of the eyelid, not from its margin. This point is

¹ *Palaeobiologie*, 1912. Also Mivart, *The Frog*, 1881, p. 93.

² Schwalbe: *op. cit.* supra, for reference, see p. 65.

best appreciated when vertical sections of the lids (such as the preparations in the Cambridge Collection) are examined.

(2) The frontal hair (cf. Fig. 53) in *Tarsius* is directed caudo-cranially: three divisions are recognized. Herein *Tarsius* stands in marked contrast with most Lemurs, and indeed resembles Man himself.

(3) The source of this stream or series of hair-tracts is like that of the Lemur in so far as it is nuchal in position (Fig. 54). But it is single and median, contrasting in both respects with the Lemurine arrangement.



Fig. 53. *Tarsius spectrum*. Scheme of the hair-tracts on the face and scalp. (From Schwalbe.)

(4) No spiral vortices are to be seen on the flank in *Tarsius*, and again a difference from the Lemur has to be recorded here.

(5) Spirals are present however in the pectoral region of *Tarsius* (but absent from that situation in Lemur).

(6) Finally the region of the elbow must be noted (Figs. 54 and 55). In *Tarsius* the hair streams down over this region towards the forearm and wrist without interruption. In the Lemur convergent tracts meet in this part. The series of contrasts thus enumerated will serve to indicate the independent position of *Tarsius* in respect of the hair-tracts.

The implantation of the hairs¹ is in general by groups of three. The tail is however exceptional, for the grouping is lost in this part.

¹ De Meijere, for reference see p. 67.

C. **The Skin.** In specimens preserved in formalin, the skin where exposed has a light yellow tint. It is darker on the plantar aspect of the foot, and still darker on the palmar or volar surface of the hand. The lack of pigmentation at the sites of the vibrissae about the face has been noted in the preceding section (B).

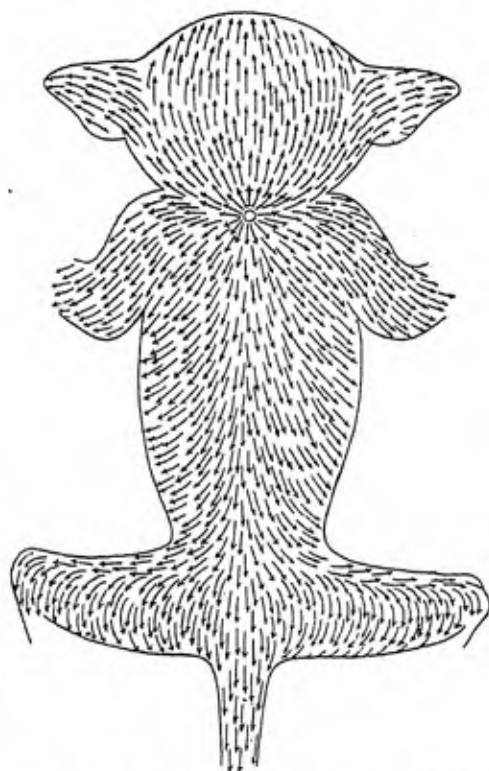


Fig. 54. *Tarsius spectrum*. Scheme of the hair-tracts on the dorsal aspect of the body. (From Schwalbe.)

True scales are said to occur on the ventral surface of the tail. In that position I have observed a cutaneous patch, but this resembled the palmar and plantar surfaces for it was marked by cutaneous grooves in two convergent series.

D. **The hands and feet** (Figs. 56 and 57) bear distinct pads on their ventral (flexor) aspects. Moreover the surface is rather

more completely covered by such pads than is the case in the Lemur. Five apical pads are to be seen in hand and foot alike. Of the interdigital pads, all four are observed on the hand, but only two on the plantar surface of the foot, where the second has joined the third, and the fourth is merged in the "antithenar" pad. On the vola (palm) two proximal pads appear, and that on the thenar side is continuous with the first interdigital pad. On the plantar surface the two proximal pads have united towards the heel and thus form a V-shaped mass. On the whole, the primitive distribution of the pads is still clear. Between the pads, small nodules are present, though these are much less numerous than in the Lemur. Papillary ridges are found on the pads and on the nodules, and Schlaginhaufen considers that the extent of surface thus marked by ridges is greater relatively in *Tarsius* than in

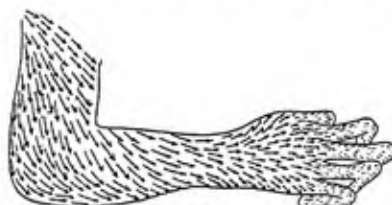


Fig. 55. *Tarsius spectrum*. Scheme of the hair-tracts on the upper limb. (From Schwalbe.)

Lemurs. If this be so, the higher position is to be accorded to *Tarsius*.

The apical pads are marked in a fashion closely resembling the pattern already described for the Lemur (cf. *supra* p. 71). But the sinus primarii (on the strictly ventral aspects of these pads) have been subjected to a curious torsion in their relation to the terminal loops marking the extreme tips and the dorsal aspects (Schlaginhaufen, *op. cit.* fig. 102 c). On the palmar surface the proximal and interdigital pads (Fig. 56) bear slightly-curved ridges with two "tri-radial" at most. The phalangeal surfaces are similar in marking to those of the Lemur. Specimens of *Tarsius* at Cambridge shew a more extensive area thus distinguished (on the phalanges) than the example figured by Schlaginhaufen, but the second digit is (in both cases) less marked than the others.

It is uncertain whether the ridges in *Tarsius* are developed from *insulae primariae* or *insulae lenticulares* (cf. *supra* p. 71)

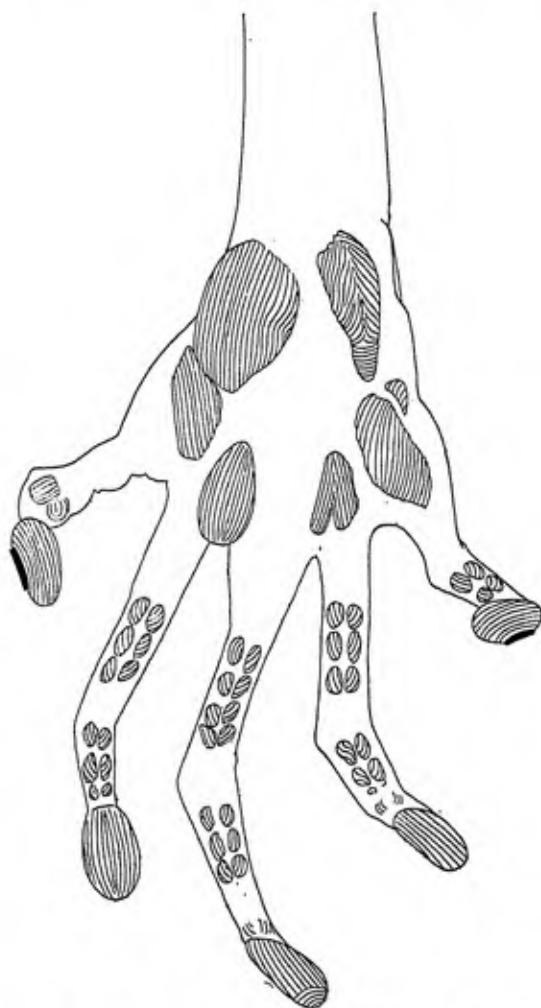


Fig. 56. *Tarsius spectrum*. (Mus. Anat. Cant.) Scheme of the cutaneous pads on the palm of the hand. ($\times 4$ approx.)

though I have some evidence suggestive that the former source is the real one.

In this place it is convenient to note again that the ventral surface of the tail of *Tarsius* bears in two places naked ridge-marked areas. The ridges are convergent towards each other in the mid-ventral line and this convergence is towards the tip of the tail, *i.e.*

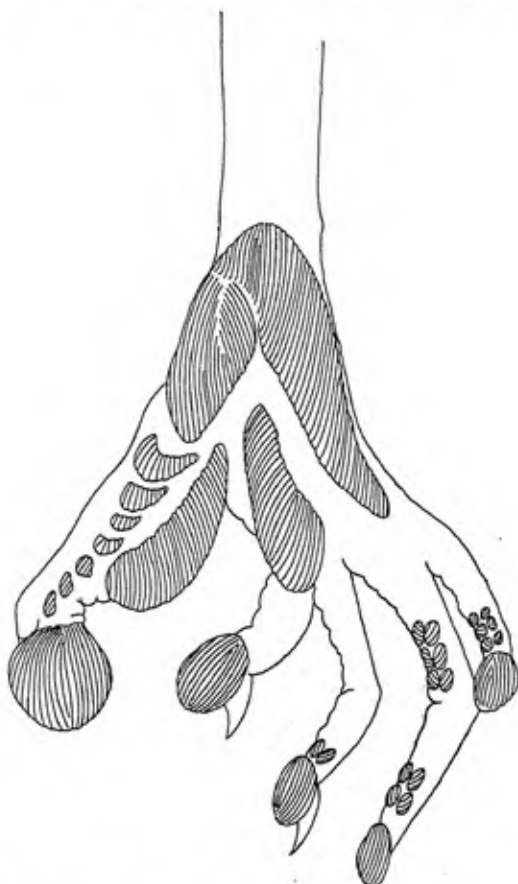


Fig. 57. *Tarsius spectrum*. (Mus. Anat. Cant.) Scheme of the cutaneous pads on the sole of the foot. ($\times 4$ approx.)

distal as regards the trunk (v. however the description of caudal scales p. 99 *supra*).

E. The Skeleton. The skull (Figs. 58 and 59) presents several features in which *Tarsius* is contrasted with the true

Lemurs. (Among the latter, certain less typical forms, such as *Loris*, make some approach to *Tarsius*.) Some of these points of contrast are foreshadowed by the form of the head and by the physiognomy in general. Considering the latter first, we notice that shortening of the jaws is characteristic of *Tarsius*. But as regards the nose, the skeleton fails to indicate the distinctive feature of this part of the face, viz. the wide separation of the nostrils, which are directed laterally away from each other.

In accordance with expectation, the orbital cavities are large to the point of grotesqueness. The space between them is re-



Fig. 58.



Fig. 59.

Fig. 58. *Tarsius spectrum*. The cranium in profile (nat. size).

Fig. 59. *Tarsius spectrum*. Frontal view of the cranium. ($\times 2$.)

duced to a mere film-like septum recalling the conditions in a bird's skull. The cribriform plate of the ethmoid does not exist as such, and it is stated (Burmeister) that the olfactory nerve-filaments pass to the nasal fossa by a single canal on each side.

The form of the palate differs from that of the Lemurs in its proportions, for it is short, and, though wide posteriorly, it becomes suddenly narrow at the level of the second post-canine tooth.

The glenoid fossa appears to be slightly deeper than in the Lemurs. The tympanic region provides good evidence of the distinctive position of *Tarsius*. For although the enormous bulla is provided by the "endotympanic" element (as in Lemur), the

tympanic annulus is not enclosed in it. On the contrary, the tympanic bone is widened to form a short funnel-shaped cylinder and by this the osseous external auditory meatus is surrounded¹. (In this respect, *Tarsius* agrees with the true apes.) But even this does not exhaust the list of peculiarities exhibited in this region of the cranium of *Tarsius*. For the entrance to the carotid canal is situated far in front of the stylo-mastoid foramen, and on the ventral aspect of the auditory bulla. The latter is "endotympanic" in origin (as already noted) but it seems to have shared in the changes determined by the enlargement of the eyes. Weber (quoted by Kampen) ascribes to that enlargement the displacement of the foramen magnum towards the palate. And this is supposed to have caused a corresponding displacement of the auditory bulla. Such changes are therefore clearly related to the specialization of the sense of sight which is so marked in *Tarsius*.

The basal and cranial sutural lines tend to disappear in *Tarsius* earlier than in the Lemurs, and in this respect some resemblance to the avian cranium may be perceived. Again the post-orbital wall (to which the alisphenoid makes a distinct contribution) constitutes a resemblance to the Anthropoidea, and severs *Tarsius* from the Lemurs.

Lastly the teeth must be cited as absolutely distinctive; but they serve to place *Tarsius* in a relatively lowly position. The dental characters are so remarkable as to call for separate treatment and this will be accorded to them in a later paragraph.

Against the points thus enumerated as distinguishing *Tarsius* from the Lemurs, another series will now be set out as a simple list. These are the characters in which the two sub-orders are in agreement. Thus in *Tarsius* and the Lemurs alike, we find that:

1. The infraorbital canal is not roofed over in the floor of the orbital cavity.
2. At the pterion, the alisphenoid articulates with the parietal bone.
3. There is a small post-glenoid tubercle, as well as a post-glenoid fossa.

¹ Cf. Kampen, *Morphologisches Jahrbuch*, Band xxxiv. 1905, p. 678.

4. The nasal duct is placed on the facial surface and entirely outside the orbital cavity. This denotes extensive development of the "pars facialis" of the lachrymal bone.

A review of the cranial characters of *Tarsius* indicates that features of specialization are the more prominent. These are most easily intelligible if regarded as adaptations to particular conditions. A few suggest the derivation of the higher cranial type of the *Anthropoidea*. As for primitive features, they are probably most distinct in the system to which a few words must now be devoted, viz. the dentition.

As a whole, this is decidedly primitive or archaic¹ in *Tarsius* (Figs. 58 and 59). There is no gap (between the upper incisor teeth) such as that which is so distinctive of the *Lemurs*. Moreover the incisors are not pro-cumbent, but erect, and the series of small sharply-pointed conical teeth in the front of the mouth (extending to the first premolars inclusive) produces a strong resemblance to the dentition of the *Insectivora*². The upper molar teeth bear three cusps only, while in the lower molars, the three cusps are supplemented by a "heel" or "talon" (for further details cf. Chapter VI).

The two halves of the mandible are joined by synostosis at the mental symphysis, and thus the condition found in the *Anthropoidea* is recalled.

Vertebral Column. A skeleton of *Tarsius spectrum* in the Cambridge Collection has the following vertebrae, viz. total 49, of which 7 are cervical, 13 thoracic (according to Burmeister, 14 thoracic vertebrae may occur), 6 lumbar, 5 sacral and 18 caudal in character.

The atlas vertebra is characterized by its great size and more particularly by its width. Of the cervical vertebrae, the second or axis alone presents a distinct (though not a bifid) vertebral spine. These peculiarities may provide an explanation of the extent of rotation of which the head (in the living animal) is capable as described above.

The six lumbar vertebrae are arranged in a perfectly rectilinear series, but a distinct lumbo-sacral angle is observed in

¹ Hubrecht, *Descent of the Primates*, 1897, p. 11.

² Earle, *Natural Science*, May, 1897, p. 309: with special reference to the work of Leche.

the example mentioned above. Of the five sacral vertebrae, two articulate with the ossa innominata, though three are fused together. Two more wide vertebrae follow these, and have been reckoned as sacral, for they are contrasted with the narrow (caudal) elements succeeding them.

The clavicles are relatively large, and are curved slightly but with uniform convexity forwards.

The rod-like sternum consists of four conjoined pieces. An additional ossified portion follows, and from this a cartilaginous expansion (metasternum) is continued still further caudally. In the dissection of *Tarsius*, I found a small suprasternal process anterior to the presternum. The scapula is curiously proportioned, being very long and narrow: the coracoid process is falciform (as in the *Lemur*), and the acromion process is spatulate. The massive humerus has no deltoid eminence, but the outer lip of the bicipital groove is very prominent and elongated, so that possibly it may include that eminence. The inner lip of the groove is slightly developed.

The radius and ulna exceed the humerus in length and are not bowed apart¹ (as in the *Simiidae*).

The carpal bones include an independent os centrale, and the os hamatum surpasses all the others in point of size. The terminal phalanges of the digits are excessively short when compared with the other phalanges or with the metacarpals. The third digit is the longest.

The os innominatum is narrow and elongated, with a large thyroid foramen and a small blunt ischiatic spine. The symphysis does not extend to the ischia, but is limited to the pubic elements. The narrowness of the pelvis and the obliquity of its anterior aperture (pelvic brim) recall the conditions in the rabbit.

The femur has a straight shaft, which expands at its condylar end.

The tibia is long and slender: the head is slightly retroverted, and the shaft markedly platynemic, as befits an animal of saltatory habits (cf. *M. Vallois, op. cit., v. p. 76 supra*). The fibula is slender and though free above and below, it seems to be actually fused with the tibia just below the mid-point of its length.

¹ This does not agree with Burmeister's description.

The extraordinary elongation of the os calcis and os naviculare has been noted already. The distal phalanges of the digits are relatively very short. The nails on the second and third digits are distinct from the remainder by reason of their spur-like form and erect position. The fourth digit is the longest of all and in this respect *Tarsius* resembles certain Frogs.

F. Muscular System. In describing the more important muscles, the same system is adopted here as was employed in the case of the Lemur (*v. supra*, p. 77, footnote).

1. The *M. platysma* is fully developed, but I am unable to detect a *M. sphincter colli* in the specimen of *Tarsius* dissected. The auricular muscles are large and prominent, being thus appropriate to the enormous ears. The *M. dorso-humeralis* is also very distinct and extensive. So substantial is it, that it may be mistaken for the *M. latissimus dorsi*, on which it lies.

2. The *M. digastricus* is very different from that of the Lemur, and approaches the human form of this muscle. A thin cord-like tendon intervenes between the posterior belly (attached to the occiput), and the anterior belly. The latter contains no tendinous fibres where it is attached to the mandible, and it extends backwards from the symphysial region for a considerable distance. Here it is applied to the lower border of the jaw, but is not overlapped by that bone.

3. The *M. sterno-mastoideus* is wide and ribbon-like. In origin it is entirely sternal, and the site of its attachment extends above the presternum, the prolongation resembling that seen in *Pteropus* (Cheiroptera). The *M. cucullaris* (trapezius) barely extends to the occiput above, and its lower part is separated as a *M. depressor scapulae*. Beneath this stratum the *M. rhomboideus* is situated, as well as an aberrant slip named from its attachments *M. occipito-scapularis*, though it lies deep to the *M. trapezius* and may represent part of the *M. levator anguli scapulae*.

4. The *M. deltoideus* does not extend so far towards the vertebral border of the scapula as in Lemur, but this "spinous" portion is distinct from the rest of the muscle. The *M. pectoralis major* is entirely "sternal" in origin: at its caudal border it blends

with the sheath of the *M. rectus abdominis* (which is traceable beneath it as far as the third rib) and the *M. obliquus externus abdominis*. Otherwise the disposition of the pectoral mass resembles that noted in the Lemur.

The *M. latissimus dorsi* has no scapular component; it is greatly attenuated at its origin, merging aponeurotically with the deep fascia over the longitudinal muscles, among which the *M. spinalis dorsi* cannot be recognized. The *M. dorsi-epitrochlearis* arises by muscle-fibres from the muscular (not the tendinous) part of the *M. latissimus*, and its lower attachment (to the olecranon) is distinct.

5. The *M. biceps humeri* has the two normal heads, and of these the so-called coracoid head is closely related to the *M. coracobrachialis*. The latter muscle is twofold with a superficial portion extending far down the humerus, and a shorter deeper part inserted beneath or behind the *M. latissimus dorsi*. No *lacertus fibrosus* was seen in my specimen.

6. The *M. flexor longus pollicis* is almost independent of the *M. flexor profundus digitorum*, but (as in the Lemur) it receives a stout band of muscle-fibres from the epicondylar part of the *M. flexor sublimis digitorum*. The pollex is provided with a *M. abductor longus* and a *M. extensor longus*, but no *M. extensor brevis*. Herein *Tarsius* resembles the Lemur exactly. There is a well-developed "deep" extensor muscle for the digits 3, 4, and 5.

7. The Diaphragm is thin and the central tendon is neither extensive nor conspicuous. The crura are very distinct from the curved portion of the muscle. Arcuate ligaments are scarcely recognizable, but over the region of the external arcuate band an extensive hiatus of non-muscular tissue is found (as in Man) behind the kidney. The nerve (phrenic) appears to be distributed mainly on the thoracic aspect of the Diaphragm.

8. The *M. gluteus maximus* resembles in its origin that of the Lemur. Its extension down the femoral shaft beyond the mid-point of the femur is remarkable. The *M. adductor magnus* extends to a similar distance, but not to the internal condyle, while the other adductors together with the *M. psoas* and *M.*

pectineus are concentrated at the upper end of the bone. The *M. gluteus medius*, *M. gluteus minimus*, and the *M. tensor fasciae femoris* are described by Burmeister.

The *M. biceps femoris* is most remarkable in appearance, consisting as it does of a very long thin tendon leading from the ischium downwards to a broad muscular sheet. This tendon is stated by Klaatsch¹ to be recognizable in other forms, though embedded in the upper end of the muscle-mass. In *Tarsius* it is exposed, and with the great sciatic nerve it lies in a groove between the *M. gluteus maximus* and the *M. adductor magnus*. There is no short bicipital head, nor is the *M. tenuissimus* present.

The *M. gracilis* and *semitendinosus* are also peculiar, for though distinct and ribbon-like above, they share a thin cord-like tendon of insertion into the tibia. The *M. quadriceps extensor cruris* is remarkable for the great development of the *MM. vasti*, especially the *M. vastus lateralis* (*externus*). This is doubtless related to the leaping movements so characteristic of *Tarsius*.

Below the knee-joint, the *M. tibialis anticus* first calls for remark in view of its great size, another token of the saltatory capabilities of *Tarsius* (cf. Vallois, *op. cit.* 1912). The *M. tibialis posticus* is comparatively small, yet it is attached to the tibia and fibula as well as to the interosseous membrane. Its long slender tendon widens out below the ankle, and runs distinctly to the navicular bone (and, in the specimen dissected by me, to the sheath of the *M. abductor minimi digiti* as well). The *M. soleus* has a circumscribed origin from the fibula only.

The *M. plantaris* arises from the femur, and its tendon passes over the *os calcis* to form the plantar aponeurosis. This is supplemented by an additional band for the hallux, and from the margin of this part a few fibres are contributed to the *M. abductor hallucis*.

The plantar muscles and tendons will now be described in the same order as was adopted in the account of the *Lemur*.

(i) *M. flexor digitorum pedis brevis*. This muscle has two modes of origin, viz.:

(a) From the deep aspect of the plantar aponeurosis, which contributes the tendon to digit No. 2 only.

¹ *Morphologisches Jahrbuch*, Band xxix. 1902, p. 264.

(b) From the surface of the tendon of *M. flexor longus hallucis*: hence perforated tendons pass to digits Nos. 3, 4 and 5.

(ii) *M. flexor digitorum longus* (*flexor tibialis*). This muscle runs almost exclusively to the fifth digit, for which it provides the perforating tendon. No *M. quadratus plantae* was seen.

(iii) *M. flexor hallucis longus* (*flexor fibularis*). This muscle sends perforating tendons to digits Nos. 2, 3, 4, 5, and it gives rise to the *MM. lumbricales*.

These dispositions are so nearly identical with those in the Lemur that no further comment is necessary. The account here given is based on my dissection, but does not in details confirm the descriptions of Burmeister. The chief difference consists in the distribution of the tendon of the *flexor tibialis* (*M. flexor longus digitorum*).

The dorsal interosseous muscles of the foot appear to be disposed about the *fourth* (i.e. the longest) digit as their axis. I have found no existing record by which to check this statement, which represents the condition in the specimen dissected by me.

A general review of the musculature of *Tarsius* leads to the conclusion that it is closely related to the *Lemuroidea* in this respect. The most striking features in *Tarsius*, such as the enormous size of the *M. vastus externus* (*lateralis*) or the *M. tibialis anticus* are not absolutely distinctive, for they are clearly foreshadowed even in the true Lemurs, and in the saltatory forms called *Galago* they approach the degree of specialization attained by them in *Tarsius*.

G. Vascular System. The Pericardium is even less extensively attached to the Diaphragm than in Lemurs¹. The aortic arch gives off the great arterial trunks in a sequence and manner identical with that found in Man, so that the higher position of *Tarsius* in this respect must needs be admitted. The internal carotid artery enters the tympanic bulla in an unusual position (*v. supra* in the note on the skull), but according to Kampen, the stapedia artery is given off as in the Lemurs. With regard to the arteries

¹ For a similar conformation occurring anomalously in Man, cf. Turner, *J. A. P.* Second Series, 1870, p. 114.

of the limbs, I may note that in my specimen the brachial vessel¹ bifurcated high up in the limb, giving rise to a superficial branch becoming the radial artery, and a deep division which in company with the median nerve passed through the entepicondylar foramen to become the ulnar vessel. According to Burmeister, the brachial artery itself passes through that foramen, and bifurcates distally to it. In the lower limb, a breaking up of the femoral artery to form a rete mirabile has been described by Vrolik and by Burmeister. In the lower part of the thigh, I have observed two main vessels, one of which is the superficial femoral artery, while the other represents the arteria anastomotica which is in *Tarsius* of large size as in the Apes.

H. The Nervous System: the Brain² (Figs. 60—64 incl.). In entering on a brief account of the brain of *Tarsius*, the same



Fig. 60.

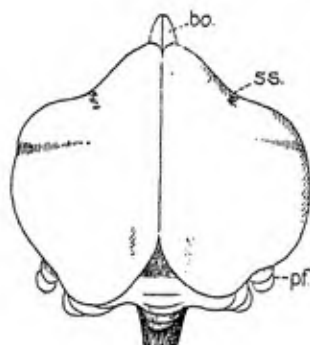


Fig. 61.

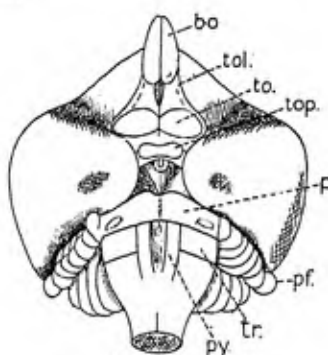


Fig. 62.

Figs. 60, 61, 62. Brain of *Tarsius spectrum*. Indications as follows: *Ss.* sulcus suprasylvius. *bo.* bulbus olfactorius. *pf.* paraflocculus. *tol.* tractus olfactorius. *to.* tuber olfactorium. *top.* tractus opticus. *p.* pons. *tr.* trapezium. *py.* pyramis. Fig. 60, Left lateral view, nat. size. Fig. 61, vertex, and Fig. 62, basal view, $\times 2$. (After Elliot Smith.)

¹ The rete mirabile described by Göppert (as quoted by Manners Smith, *J.A.P.*, 1911) was not identified.

² Cf. especially Elliot Smith, *Trans. Linn. Society of London*, Vol. viii. part 10, 1903, p. 370.

preliminary considerations are to be borne in mind as in the case of the Lemuroidea (*v. supra*, p. 85).

(i) The cerebral characters undoubtedly include some which may be described without hesitation as primitive. It is noteworthy that in *Tarsius* such characters are found to be related to the commissures of the hemispheres. Of these, the corpus callosum provides the most striking example, for its extent in an antero-posterior direction is remarkably small. The cerebellum also falls within this category.

(ii) Primitive or pseudo-primitive features accountable to processes of reversion or degeneration are not generally recognized.

(iii) The large size of the eyes, consequent upon the adaptation of *Tarsius* to nocturnal habits, has produced a most marked effect on the general form and proportions of the cerebrum, both directly and indirectly.

(iv) *Tarsius* is a very small mammal, and as such it provides evidence confirmatory of the general rule that in the smallest forms, the complexity of cerebral convolutions is far less than in larger representatives.

The details now to be added will involve further elaboration of these general principles. The cerebrum of *Tarsius* (Figs. 60—64 incl.) is remarkable in form and proportions. Viewed from above it is broader than it is long, and the surface is devoid of all sulci save a slight impression (Fig. 60, *ss*) identified with the *S. suprasylvius*.

When examined from one side, the hemisphere (Fig. 60) is marked in front by a deep and extensive fossa where it rests on the orbit. The occipital end also bears an impression on its ventral aspect where it extends over the cerebellum to a considerable extent.

The rhinencephalon comprises a small sessile olfactory bulb of "triticeal" form, a short wide peduncle, a (relatively) small pyriform lobe, with a small tuberculum olfactorium. The rhinal fissure is not usually distinguishable. On the whole, the rhinencephalon stands mid-way between those of the Lemuroidea and the Anthropeidea.

Of the marginal pallium, the most distinctive feature is provided by the direct passage of the gyrus dentatus towards the splenium of the corpus callosum, no sub-splenial flexure being present. In no Lemur or Ape is this arrangement found, and for a comparable disposition of parts, the lowly brain of the Sloth must be examined. The determining factor is the small extent (backwards) of the corpus callosum, and the limitation of growth in this commissure stamps the brain of *Tarsius* as one of the most primitive among those of Eutherian mammals.

The general form of the neopallium has been described above. The deep orbital excavation is indicative of the enormous eyes. With these is to be associated the remarkable occipital prolongation of the neopallium behind the corpus callosum, and over the cerebellum. In this prolongation an extensive posterior cornu



Fig. 63. *Tarsius spectrum*. Mesial aspect of the cerebral hemisphere. (After Elliot Smith.) $\times 4$.

of the lateral ventricle is situated. As might be anticipated, the area striata (visual area) of the cortex is extensive. The histological features of this area, and indeed all the features just enumerated as distinctive of the occipital region, separate *Tarsius* from the Lemuroidea, bringing it at the same time into relation with the lower Anthroipoidea.

The various areas of the neopallial cortex are exhibited in a diagram (Fig. 64) based on a sketch which I owe to the kindness of Professor Elliot Smith. To the same authority I am indebted for sketches from which Figs. 65 and 66 have been prepared. These represent two types of brain in the Insectivora, and taken together with Fig. 64, they provide a graphic illustration of the evolution of the neopallium. But it is to be understood clearly that the indications are of a general nature only, and that the charts are not necessarily precise in detail.

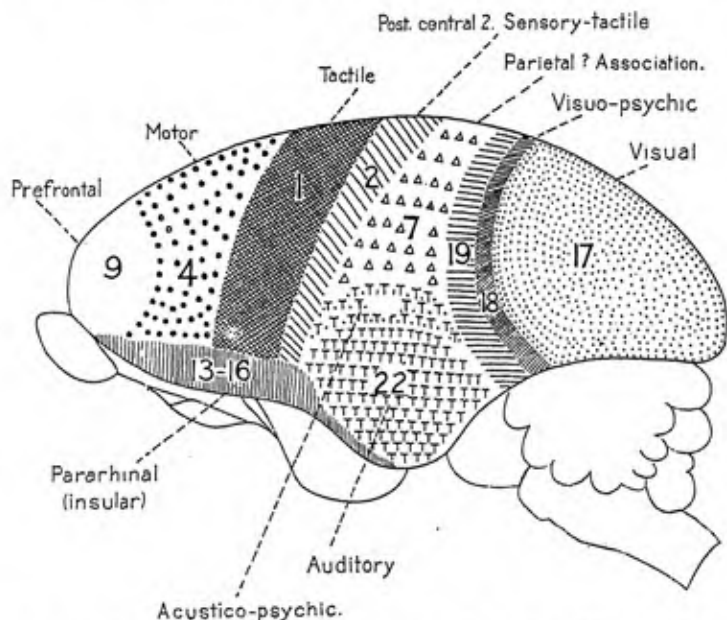


Fig. 64. *Tarsius spectrum*. Cortical areas of the brain. This figure is based upon a sketch by Professor Elliot Smith. The numbers have been added tentatively by the writer. They provide for the comparison of the brain of *Tarsius* with that of the *Lemur* (Fig. 46) and with other brains described in the sequel. Attention is directed especially to the areas marked 1, 4 and 17 respectively, corresponding to those named by Brodmann as follows:

- No. 1. Area post-centralis.
- No. 4. Area giganto-pyramidalis.
- No. 17. Area striata. (Elliot Smith.)

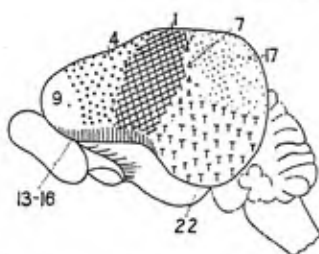


Fig. 65.

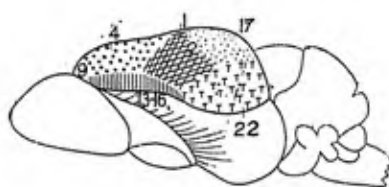


Fig. 66.

Fig. 65. *Tupalia* sp.? Cortical areas of the brain (from a sketch by Professor Elliot Smith).

Fig. 66. *Macroscelides* sp.? Cortical areas of the brain (from a sketch by Professor Elliot Smith). These brains of Insectivora, together with that of *Tarsius* (Fig. 64), serve well to illustrate the evolution of the cortical areas, and the general form of the brain.

In regard to the commissures, sufficient note has been taken already of the corpus callosum. The anterior commissure is relatively large, and the dorsal commissure (psalterium) is not so diffused as in the other Primates. The representative of the sulcus suprasylvius has been mentioned already. Other impressions on the hemisphere are the fissura hippocampi, together with the representatives of the sulcus calcarinus and sulcus paracalcarinus (on the mesial aspect). (Cf. Fig. 63 and references: *fh.* fissura hippocampi. *sc.* sulcus calcarinus. *spc.* sulcus paracalcarinus. *src.* sulcus retrocalcarinus.)

The cerebellum approaches the form characteristic of that organ in the Insectivora, more nearly in *Tarsius* than in any other of the Primates. Yet the relatively higher degree of folding in the cerebellar cortex, and the more massive "middle lobe" in *Tarsius*, shew that this form has advanced already beyond the lowlier stage presented by the Insectivora.

The hypophysis or pituitary body of *Tarsius* consists of a median non-glandular portion with two lateral lobules, which are glandular. The glandular parts are said to lie above the diaphragma sellae turcicae. The distinction of a median lobe from two lateral lobules is characteristic of Reptiles. And so far as is known, the Primates alone among Mammals retain this feature. For other details, the memoir by Bolk¹ should be consulted.

In the preceding notes reference has been made to distinctive characters of the brain which are indicative of a primitive type of conformation. Again, certain features are seen to be associated with special developments, such as that of the eyes. Lastly, the absolute size of *Tarsius* must be taken into account. The smooth-surfaced neopallium might seem capable of interpretation by an appeal to this factor alone. Yet since the Lemurs fortunately include certain representatives similar in bulk to *Tarsius*, that interpretation is shewn to be inadequate, and the neopallium of *Tarsius* is seen to possess the character of smoothness in a degree inappropriate to even Lemurine rank. On the other hand, the fissuration of the cerebellum demands a similar comparison.

¹ Konink. Akad. van Wet. Amsterdam, Dec. 24, 1910.

As a result of this, *Tarsius* is not lowered in position when the smallest Lemurs are employed as the standard.

But the curious combination of primitive with advanced characters confers upon the brain of *Tarsius* an interest hardly to be equalled among its congeners.

I. The Organs of Respiration. The Lungs. The distinctive character of these organs is the multiplicity of the lobes, for the



Fig. 67. *Tarsius spectrum*. Vertical coronal section of the larynx, through the anterior part of the plica vocalis. The m. crico-thyroideus does not pass far up inside the thyroid cartilage here, but further back it does so. 1, extreme margin of the epiglottis in the plica ventricularis; 2, appendix laryngis; 3, hyoid bone; 4, thyroid cartilage; 5, cricoid cartilage; 6, m. thyro-arytenoideus; 7, m. crico-thyroideus. ($\times 8$.)

right lung has five lobes (including a lobus impar), the left lung being divided into four parts. The tracheal rings are complete (as in the Lemurs, excepting the *Galagos*).

The Larynx (Fig. 67). The form of the epiglottis approaches that of the Lemurs. In respect of other features *Tarsius* must, however, be contrasted with those animals. For the examination

of coronal sections (Fig. 67) shews that the free portion of the plica vocalis (true vocal cord) is small, while the musculature adjacent to it is very extensive and less differentiated into separate masses. Such characters may be claimed reasonably as evidence of a lowly or primitive status.

J. The Alimentary Canal. The lower lip (Fig. 69) of *Tarsius* differs from that of Lemurs and Apes alike in the possession of exceptionally large and extensive sebaceous glands.

The hard palate is marked by transverse ridges or rugae, which are not limited to the fore part but cross the roof of the mouth at intervals along the whole of its extent.

The stomach forms a simple dilatation of the intestinal tube, having a greater and a lesser curvature. The latter is closely fitted round the papillary portion of the lobus descendens (lobus caudatus of many writers).

The Liver (Fig. 70) presents the following noteworthy features:

(a) While resembling the Lemurian liver in general characters, and holding consequently but a lowly position, the liver of *Tarsius* does not shew the excess of lobulation met with in at least some Lemurs. In the specimen I examined there is a greater tendency to the production of small lobules than is implied in the account given by Ruge (*op. cit. v. supra*, p. 90, footnote). But I cannot recognize a fissura umbilicalis. Leche (quoted by Ruge) states that it is absent.

(b) The mode of fixation to the diaphragm and abdominal wall is almost identical with that described in connexion with the Lemur.

(c) In the liver of *Tarsius* the incisura oesophagea is so shallow that a great contrast exists between this animal and the Lemur in this respect.

(d) The incisura duodenalis is seen to be present but is reduced greatly both in width and depth.

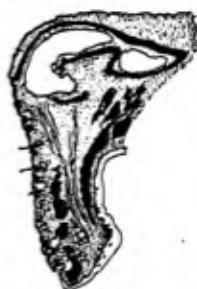


Fig. 68.



Fig. 69.

Figs. 68 and 69. Sections of upper and lower lip. Adult *Tarsius spectrum*, ♂.

(e) The left lateral lobe (Fig. 70) resembles that of the Lemur, for it sweeps round to the right side of the abdominal cavity.

(f) The lobus caudatus has a very distinct papillary component (lobus Spigelii) which fits accurately into the lesser curvature of the stomach, being clearly visible from the ventral side when the left lateral lobe is raised. The "true" caudate com-

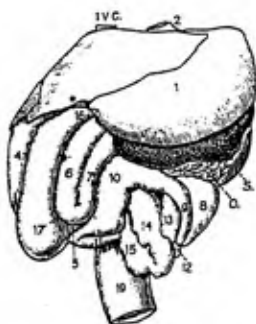


Fig. 70.

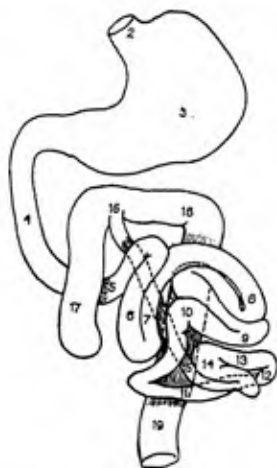


Fig. 71.

Fig. 70. *Tarsius spectrum*. The abdominal viscera in their natural relations. References to numbers as follows:

1. Left lobe of liver.
2. Cardiac end of stomach with oesophagus.
3. Stomach.
- 4-16. Small intestine.
17. Caecum.
- 18, 19. Large intestine.
- I.V.C. Inferior vena cava.

Fig. 71. *Tarsius spectrum*. The coils of the alimentary canal. References to numbers are as in Fig. 70. (Mus. Anat. Cant.)

ponent is shorter than in the Lemur; it is neither falciform nor uncinat as in that animal. It is partly fused with the right lateral lobe (my specimen confirms this, the view of Leche, as against that of Ruge¹). In these characters (f) *Tarsius* approaches the Apes.

On the whole, however, the liver of *Tarsius* is of Lemurian type, and indeed, the aberrant Lemurs such as *Perodicticus*

¹ *Morphologisches Jahrbuch*, Band xxix. 1902, p. 527.

provide connecting gradations between the two types. Where contrasts exist, as in (c) (d) and (f), the higher type met with among the true Apes is suggested. Indeed resemblances to the most highly developed of these are not entirely absent. Yet it is not necessary to assume that *Tarsius* occupies an elevated position on this account, and it is preferable to regard it as a generalised form, representative of ancestors which can be made known only (if indeed at all) by the discovery of their fossilized remains.

The Pancreas is placed obliquely, the left extremity being lower than the head.

The Duodenum (Figs. 70 and 71, No. 4) resembles that of the Lemurs in position but is less prominent. The disposition of the coils of the small intestine is shewn in the accompanying illustration. It will suffice to notice the comparative simplicity of this part of the alimentary canal.

The Caecum (Figs. 70 and 71, No. 17) is of very considerable dimensions and no appendix is to be distinguished. The large intestine consists of a short straight transverse colon and a rectum.

The Spleen is placed between the diaphragm and the stomach, having less extensive relations with the left kidney than is the case in the Lemur.

K. Urogenital Organs. The left kidney is placed more caudally than the right. Into the pelvis of each kidney, four pyramidal eminences (one far larger than the rest) were seen (by Burmeister) to project. The right suprarenal body is placed high up behind the liver, and in a specimen of *Tarsius* dissected by me it was supplemented by a small accessory suprarenal body placed in front of the hilum of the right kidney. The left suprarenal was not at the upper pole of the kidney and did not appear above the upper border of the pancreas. The testes are intra-abdominal in a male *Tarsius* dissected by me. (They unfortunately yielded no sperm-cells capable of separation for examination by Retzius' method.) In the penis of *Tarsius*, the intercavernous septum does not contain cartilage, but only fibrous tissue. This applies at least to the anterior part, where the corpus spongiosum is not to be recognized. The uterus is bicornuate (Burmeister), and the clitoris terminates in a large glans clitoridis. In this respect *Tarsius* appears to resemble the Lemuroidea.

III. ANTHROPOIDEA.

As is well known, this Sub-order includes a large variety of forms, differing in respect of geographical situation, habits, external form, and last, but by no means least, of intellectual development and temperament. In the chapter dealing with classification, the main divisions, viz. the New World apes (Platyrrhinae) and the Old World group (Catarrhinae) including Man himself, have been indicated already. In the present place, a selection has to be made, and only examples of the Catarrhinae are described in detail. Among the Catarrhinae, representatives of the Cercopithecidae and Simiidae will now be considered.

(i) *Cercopithecidae*.

The Family Cercopithecidae itself consists of an assemblage of many and diverse animals. We may consider as typical the members of the genus *Cercopithecus* from which the Family has received its designation. The very name (*Cercopithecus*) is not without interest. Since it signifies an ape with a tail, we may infer that apes lacking or apparently lacking that distinctive appendage were known already to those who coined the name. Perhaps they need not have travelled far to see such apes, for those found in Barbary and at Gibraltar are to all outward appearance tailless¹. Modern systematists include these apes in the genus *Macacus*. The Macaques are nearly related to the Cynocephalous apes, one point of resemblance being that of habitat in the sense that they are found almost as frequently in rocky scrub-covered districts as in the forest-covered areas².

The true *Cercopithecus* is however a typical arboreal form. Rivalling the Lemurs in activity and agility, it resembles them further in the highly specialized state of the visual organs, and indeed surpasses them in the extent to which vision has become binocular through the more complete overlap of the visual fields.

¹ An early memoir on the comparison of Man and Apes is that published in 1572 by Coiter. *Analogia ossium humanorum simiae et verae et caudatae quas Cynocephali similis est, atque vulpis*. Notice that a distinction between "true" and "tailed" apes is recognized.

² Cf. statements quoted in regard to *Lemur catta* amongst the Lemuroidea.

Unlike the nocturnal Lemurs, the Cercopithecids move abroad in daylight, and such a change in habits surely provides a suggestion as to the possibilities of evolutionary progress.

Almost as impressive as the development of the apparatus of vision, is the reduction of the organ representative of the sense of smell, and it is probable that that of hearing has also degenerated to some extent. By way of compensation, some refinement of the tactile sense is inferred from the conformation of certain parts of the skin. Finally the brain is relatively large in size, and if a balance be struck between the gains and losses experienced by the various organs of sensation outlined above, the brain-mass may appear unduly great. The clue to this difficulty will be found in a study of the so-called "association areas" of the cerebral surface. These also have increased in extent. Such an increase is indicative of the advancing development of the faculty of associating sense impressions, of powers which through evolution culminate in an intellect of human type. Yet the Cercopithecids are far from having attained that stage, and while the variability of these animals may be remarked once more, it is also to be remembered that if we judge of their behaviour and mode of life from the standpoint of the ordinary observer, we must admit that many of them do not seem to have advanced far beyond the Lemurs.

In the following paragraphs the detailed descriptions are based mainly upon the conditions noted in specimens of the genus *Cercopithecus*. But in some instances (which will be indicated) recourse has been had to more accessible material, viz. examples of the genera *Macacus*, *Cynocephalus* and *Semnopithecus*. The Cercopithecids are characteristically African in their geographical distribution, while the genus *Macacus* is typically Asiatic. The Cynocephalous apes are encountered in Arabia and Abyssinia, i.e. in an intermediate area, but since they are distributed through the length and breadth of Africa, their relations are with that continent rather than with Asia.

A. General External Characters. The species of the genus *Cercopithecus* amount in number to about forty, and consequently the description of their external characters, if brief, must be of a general nature only.

The Cercopithecids are small monkeys, measuring usually in length some eighteen to twenty inches exclusive of the tail which is characteristically at least as long again as the body of the animal. The tail is not prehensile in the strict sense of that expression, which is properly exemplified by certain monkeys of the New World.

The body and tail are clad with hair which is of a bright colour and so variegated as to provide an important basis of classification¹. Individual hairs tend to reveal a banded distribution of pigment, a feature common to many groups of the Primates. Tufts of longer hairs may develop on the head, and in some species a definite beard is distinctive. The hind-limbs do not exceed the fore-limbs greatly in length, and in all cases the thumb, though short, is present (it is reduced to the merest remnant in the allied group of Colobus monkeys). The fingers shew a tendency to develop interdigital webs. The head is rounded, the face varying in prominence according to age and sex, for it is relatively largest and most prognathous in aged males.

The eyes are of large size and darkly pigmented in all varieties. The ears² are relatively smaller than in the Lemurs, and the ear-tip is not constantly present. Thus the auricle is involved in a process of reduction, which has affected the genus *Cercopithecus* more distinctly than the allied genera *Macacus* and *Cynocephalus*.

The nose is flattened and the nostrils are usually separated by a narrow septum only (in the Colobus monkeys the interval between the nostrils may be nearly as wide as in the New World monkeys).

The possession of large cheek-pouches is a very distinctive feature of many Old World monkeys and the Cercopithecids are thoroughly representative in this respect. They also possess hard callous pads devoid of hair on the buttocks in situations corresponding to the tuber ischii of each side.

¹ Perhaps the most remarkable variety is a snow-white form found on the Upper Congo. The skin is as white as the hair, but these monkeys are not albinos, for the eye-pigment is retained in the iris and even on the sclerotic coat. The occurrence of white-skinned monkeys in an area occupied by the most darkly-pigmented Hominidae affords material for free speculation. Here I will only suggest that the dim light of the more dense forests may have contributed to the production of the variety in question.

² Cf. Keith, *Nature*, Nov. 7, 1901, pp. 19, 20.

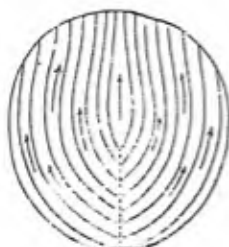


Fig. 72.

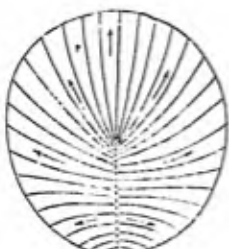


Fig. 73.

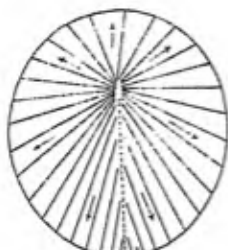


Fig. 74.

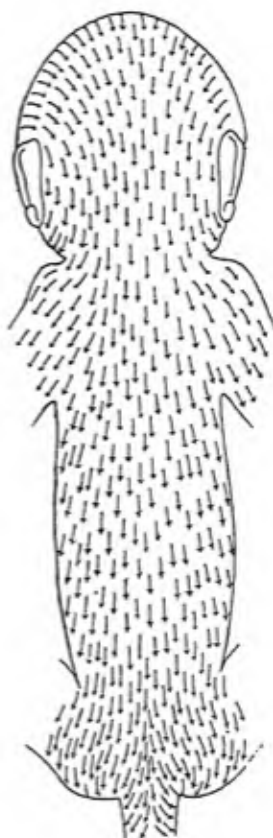


Fig. 75.

Fig. 72. *Macacus cynomolgus*. The hair-tracts of the scalp. The forehead is directed downwards. (From Schwalbe.)

Fig. 73. *Hylobates* ? sp. The hair-tracts of the scalp. The forehead is directed downwards. (From Schwalbe.)

Fig. 74. *Homo sapiens*. The hair-tracts of the scalp. The forehead is directed downwards. (From Schwalbe.)

Fig. 75. *Macacus cynomolgus*. Hair-tracts of the dorsal aspect of the head and trunk. (From Schwalbe.)

B. **The Hair.** The following notes are based on the descriptions of Schwalbe¹, who has provided admirable accounts of foetal specimens of *Macacus cynomolgus*:

(a) Sinus-hairs or vibrissae are found in four regions of the head, viz. the supraorbital region, the lateral nasal region, and near the upper and lower lips. No such hairs are found on the cheeks (cf. *supra*, p. 65). Elevations of the skin or pads of implantation for these hairs are not definitely present, though some indications were noted.

(b) From the region of the brows the hairs of the scalp are directed from before backwards, i.e. cranio-caudally; near the vertex the stream passes into a vortex in the middle line but the

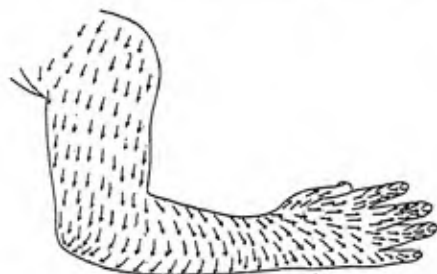


Fig. 76. *Macacus cynomolgus*. Hair-tracts of the upper limb. (From Schwalbe.)

lateral parts are not interrupted (Fig. 72, with which Figs. 35, 73, and 74 are to be compared).

(c) This caudo-cranial stream is a primitive possession. It continues (Fig. 75) without interruption along the back and on to the tail where (with rare exceptions) it divides into symmetrical lateral subdivisions.

(d) No spirals are present on the flanks.

(e) No spirals interrupt the hair-stream in the upper pectoral region (contrast with *Tarsius g.v.*).

(f) The elbow marks the convergence of two streams, one coming from the upper arm, the second from the forearm (Fig. 76).

¹ Selenka's "*Studien*," Lieferung x, 1911.

In regard to the implantation of the hairs by groups, De Meijere¹ remarks that such groups are present, and that in the Cercopithecidae they consist usually of more than three hairs.

C. Skin Colour. The skin is subject to nearly as many variations of colour as is the hairy covering of the Cercopithecii. One subdivision depends in fact for its recognition on the intense pigmentation of the extremities, for in this particular group they are of a livid colour. In other examples local patches of skin assume tints of extraordinary intensity, as for instance the green coloration of the external genitalia in *Cercopithecus callitrichus* (the "green" monkey), the dark indigo blue of the same region in *Stairs' Cercopithecus*, or the *C. cynosurus*, and again the scarlet hue of the ischial callosities in the latter species. The "flesh-colour" of the skin in Hamlyn's *Cercopithecus* has been noted already, and though this tint is universal in that animal, other Cercopithecii exhibit localized areas of similar colour.

This variability in the Cercopithecii places them in marked contrast with the (generally sombre-coloured) Lemurs.

With regard to definite scales or dermal scutes, the ischial callosities at once occur to the imagination as a possible site for such specializations. Yet, in truth, those callosities represent a hypertrophy of the epidermic squamous cells *en masse*, rather than the production of definite laminar "squamae."

D. Hands and Feet. The notes in this section are based upon the observations of Schlaginhaufen (*op. cit.*, v. *supra*, p. 69), on specimens of *Macacus*, which is the most appropriate form for consideration here.

The exposed hairless surfaces of the palm and sole are entirely covered with papillary ridges. Such an increase is distinctly suggestive of a corresponding advance in the activity of such functions as they subserve. Of the various "pads," all save the proximal "thenar" one (v. *supra*, p. 69) are represented on the vola or palm of the hand.

On the plantar surface, a prominence of the heel provides for a fresh extension of the corrugated area. All the "apical" pads are present. The four typical "interdigital" pads are also

¹ *Morphologisches Jahrbuch*, Band xxi. 1894.

developed, but have experienced a slight displacement laterally, so that they appear to be thrust towards the tibial side of their original positions. The first interdigital pad is continuous with an elongated eminence, extending nearly to the heel (and possibly equivalent to a proximal thenar pad). The fourth interdigital pad is closely connected or even continuous with a similar but narrower "fibular" eminence reaching the heel (and, in part, representative of the proximal anti-thenar pad of the primitive ground-form).

The apical pads of the digits bear patterns described as elliptical loops. On the thumb (pollex) in particular, the appearances strongly suggest the presence of the entwined loops called (by Schlaginhaufen) "vortex duplicatus." On the middle phalanges, the ridges run transversely or in flattened arches. They are less numerous here, and in *Macacus cynomolgus* they may even fail to develop in this part. On the proximal phalanges, ridges with an oblique direction mark the pollex, arches or loops replacing them in the remaining digits. On the interdigital pads, the general tendency

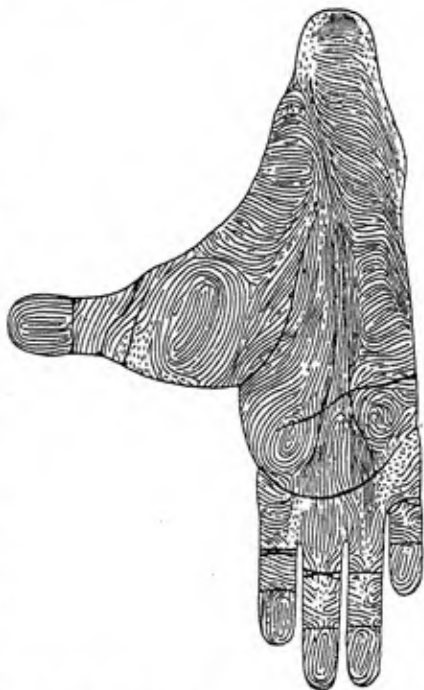


Fig. 77. *Macacus nemestrinus*. Cutaneous grooves of the sole of the foot. (From Schlaginhaufen.)

is to the appearance of "vortices duplicati" on the summit, while the spaces between the pads are marked by a series of curved lines. These originate in the "carpal" region, and radiating thence, they spread out towards the margins as they descend.

The general disposition of the papillary ridges on the plantar surface (Figs. 77, 78) resembles that just described as characteristic

of the palm of the hand. Special attention must be directed, however, to a feature ascertained (by Schlaginhaufen) to distinguish the *Macacus* group of Cercopithecidae, and with these most of the Catarrhinae including Man, while the Cynocephalous apes alone stand out in marked contrast with all their associates.

The feature in question is the course pursued by a certain line (marked R_{13a}) on the plantar surface (Fig. 79). This line (R_{13a})

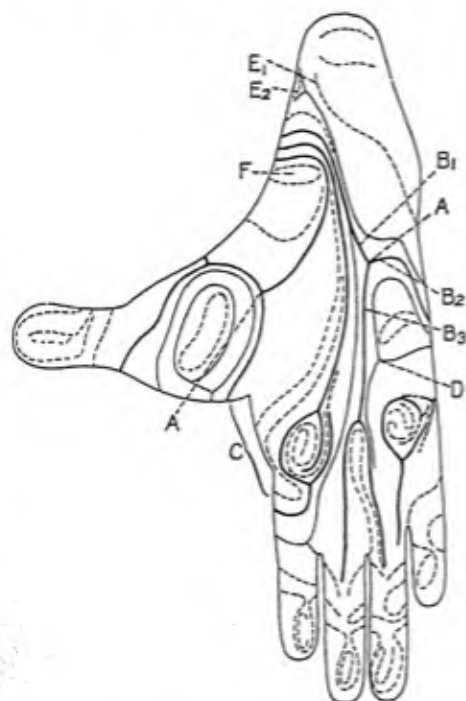


Fig. 78. *Macacus nemestrinus*. Scheme of the cutaneous grooves of the foot as shown in Fig. 77. (From Schlaginhaufen.)

- A, triradius.
- B_1, B_2 etc., lineae terminales.
- C, agmen principale.
- D, triradius secundarius.
- E_1, E_2 , agmina secundaria.
- F, figura tactilis.

should be traced from the tri-radius (T_{13}) whence it starts at the base of the first interdigital pad. It passes hence towards the heel with a bold sweep, and finally it is recurved towards the *tibial* margin. Such is its characteristic (though not invariable) course in the majority of the Catarrhinae. But in the Cynocephali it may be observed to cut clean across the plantar surface to gain the *fibular* border. (In such a case, the remaining three interdigital eminences are isolated from the proximal eminences by a series of transversely

directed ridges. The palmar surface in the Cynocephalous apes seems to be distinguished in a somewhat similar manner. It is impossible to avoid the impression that this peculiarity is associated with the eminently terrestrial habits of most of the members of this group of monkeys.)

E. The Skeleton. *The Skull* (Fig. 80). The brain-case has increased in size, particularly in its vertical diameter. The face protrudes less than in the Lemurs, but more than in Tarsius. In males (especially in aged animals) the temporal ridges are often prominent, and there may be prominent supra-orbital ridges. The snout-like projection of the facial bones is pronounced in the Dog-faced monkeys, but is much diminished in the Cercopithecini. A wall bounds

the orbit posteriorly, and the nasal duct opens within the margin of that cavity. On the inner orbital wall, the lachrymal bone is separated (as in the Lemuridae) from the os planum of the ethmoid, by the interposition of the frontal and maxillary bones which unite along a fronto-maxillary suture which often measures 10 mm. in length. The inter-orbital space is very narrow, especially in young individuals, and in its upper portion.

The infra-orbital canal is not roofed over. In the temporal fossa, the alisphenoid is separated from the parietal by the interposition of the frontal and squamous portion of the temporal bone, which unite along a fronto-squamous suture. The New-World Apes commonly present the Lemuroid feature of a parieto-sphenoid

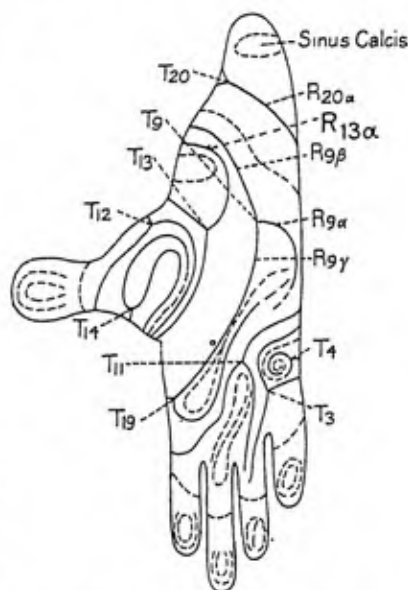


Fig. 79. *Macacus nemestrinus*. Scheme of the cutaneous grooves of the sole of the foot. Special attention is directed to the course of the line marked $R_{13\alpha}$. (From Schlaginhaufen.)

articulation. The malar bone in these apes may also be prolonged backwards so as to touch the parietal bone.

The palate is elongated, the glenoid fossa deeper than in the Lemurs; the post-glenoid tubercle is well developed and spiny. The tympanic bone is expanded to form a tube which protects the external auditory meatus and tympanic membrane, and there is no auditory bulla in the Old-World monkeys, though this feature characterizes their New-World representatives. The anterior and inferior part of the petrous portion of the temporal bone is

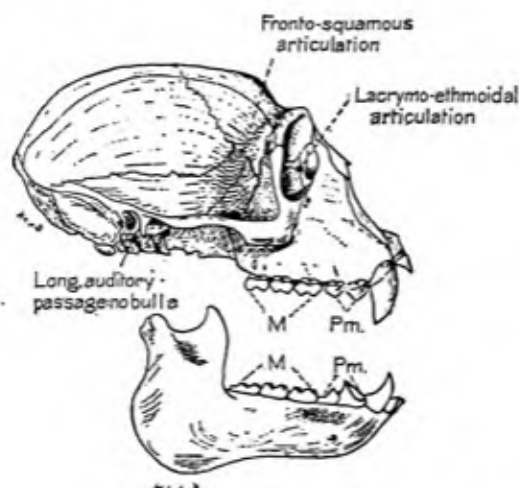


Fig. 80. Cranium, with mandible, of a *Macacus* monkey (Cercopithecidae); note the absence of an auditory bulla; the substitution of fronto-squamous and fronto-maxillary for speno-parietal and lacrymo-ethmoidal articulations; note also the number of teeth, and compare with Figs. 18 and 21.

commonly inflated in appearance. The basi-occipito-sphenoidal suture persists for some considerable time after the completion of the dentition.

The dental formula is identical with that of Man (the New-World monkeys having an additional premolar tooth in each jaw); the molars commonly bear four distinct cusps arranged in two pairs, an anterior and a posterior. (For fuller details, v. Chapter VI.)

Vertebral Column. The cervical vertebrae are seven in number, the thoracic and lumbar together are nineteen, of which twelve or thirteen usually bear ribs, and are thus to be regarded as the true thoracic elements. The tenth vertebra is often the anti-clinal element. Three sacral vertebrae and a very variable number (3—26) of caudal vertebrae complete the series. In the lumbar region, spine-like anapophysial processes (Fig. 81) are directed backwards from each vertebra to embrace the anterior zygapophyses of the succeeding one. The curvature of the vertebral column is much simpler than in Man, being a simple thoracolumbar curve whose concavity is directed downwards. Anterior to this is a cervical curvature in the opposite direction. Posteriorly, owing to a tilting upwards of the sacrum, an appearance of convexity downwards is often seen especially in the Baboons (*Cynocephali*) (Fig. 82).

The sternum consists of six ossified segments, all of which are rod-like, save the presternal element. The costal cartilages of eight ribs reach the sternum directly.

The clavicle does not shew the degree of sinuosity of the human bone. The sternal end is straight, the outer portion being concave forwards. A strong deltoid ridge replaces the tubercle of that name in the human clavicle. An impression for the *M. subclavius* is distinct.

The scapula is very broad (Fig. 83 *a*) (when measured in the general direction of the spine) in comparison with its diameter from the superior to the inferior angle: its "index" is 118 approximately. In Man, the index is about 65. The acromion process is comparatively small. The scapula in general resembles those of animals with quadrupedal gait rather than those of the Simiidae.

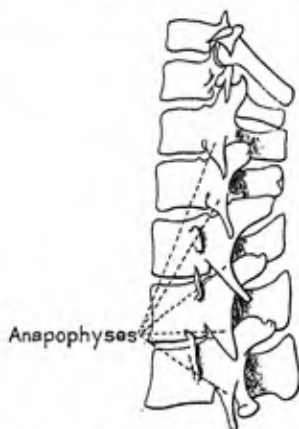


Fig. 81. Four thoracic and three lumbar vertebrae of a *Cercopithecus* monkey (*Cercopithecidae*), with anapophyses projecting laterally from the pedicles.

The outer lip of the bicipital groove in the humerus is very prominent, the inner lip being feebly developed or absent. At the lower end of the bone, the articular surface is not so sharply

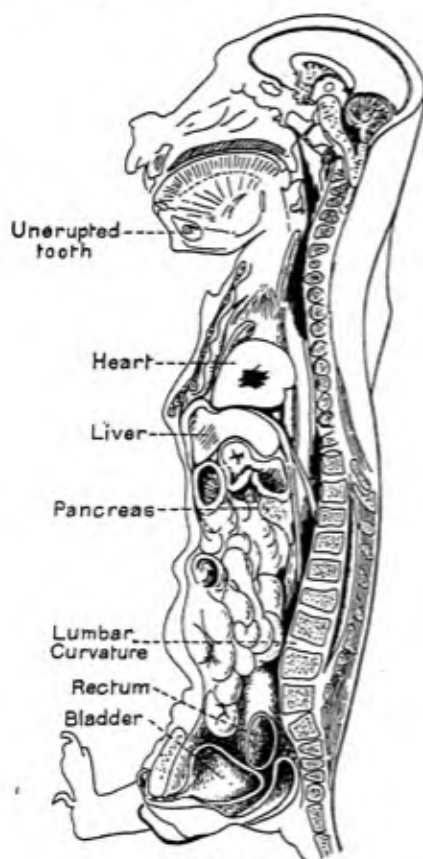


Fig. 82.



Fig. 83.

Fig. 82. Mesial section of the (frozen) body of a Cynocephalous monkey (*Cercopithecidae*). Note the enormous size of the jaws, and the comparatively small thoracic capacity and extent. The vertebral column is much less sinuous than in Man, but the anterior lumbar convexity is incipient and distinct.

Fig. 83. Scapulae, (a) of a *Cercopithecus* monkey, (b) of Man. Both have been reduced to a common denominator, viz. the transverse width.

differentiated into capitellum and trochlea as in the case of Man: the conformation of the capitellum, in particular, suggests that flexion and extension (the characteristic movements of this joint

in animals with quadrupedal structure) have not been far encroached upon by pronation and supination. The angle of torsion of the humerus amounts on the average to about 100° (cf. Broca's figures: Carnivora, average angle 95° ; European, 161°). The carpus retains a distinct os centrale: the pollex is very short, owing chiefly to the diminutive size of the phalanges.

The pelvis is transversely narrow (like the "thoracic cage"), the ossa innominata being elongated antero-posteriorly, i.e. as measured from the crest of the ilium to the tuber ischii; they thus are strongly contrasted with the corresponding bones in Man. The pubic symphysis is long, and indeed so extensive that the ischial bones come into contact. Thus the symphysis is really pubo-ischiatic. The tuber ischii is large and everted.

The femoral head is small, and the neck short in comparison with that of the human femur. There is a very distinct linea spiralis in some cases, but the linea aspera is only feebly developed. Inferiorly, the lack of transverse width is characteristic, while the curvature of the condyles, when regarded from the side, is more nearly semicircular than in the case of Man. The patella is narrow and plays equally on each condyle. Commonly a sesamoid bone is found in the outer head of the gastrocnemius muscle.

The tarsus is flattened, and its constituents similar in number to those of the human tarsus: the hallux is very short when compared with the other digits: this is chiefly due, as in the manus, to the shortness of the phalanges.

F. Muscular System¹. 1. The *M. platysma* is a strong and extensive sheet, traceable backwards to the middle line of the neck and upwards to the zygoma; below this it is attenuated locally where the cheek pouch passes outwards. In the axillary region, the *M. dorso-humeralis* is as distinct as in the Lemur or in Tarsius. In a *Cynocephalus mormon* dissected by me, nerve-fibres were supplied to this muscle from the inner cord of the brachial plexus, and also from the lateral branch of the second thoracic nerve. According to Ruge the *M. sphincter colli* is well developed.

¹ The descriptions are based partly on dissections of *Cynocephalous* monkeys. Eight subdivisions of the musculature are distinguished, and are the same as those employed in the case of the Lemur (v. p. 77 *supra*).

2. The *M. digastricus* is remarkable chiefly for the tendinous arc stretched across the middle line of the neck (from one tendon to the other). From this arcade the muscle-fibres of the anterior belly take origin, the muscles of the right and left sides forming a continuous sheet. The latter is however distinctly thick where it is attached to the mandible. Here it lies immediately beneath the lower border of the bone, but no "digastric" impression can be distinguished in the dry bone. The posterior belly is accompanied by the *M. stylo-hyoideus* which divides to allow the tendon of the *M. digastricus* to pass forward.

3. The *M. sterno-mastoideus* is massive, and it arises from the clavicle as well as the presternum. Thus two muscles are to be distinguished, and they are nearly equal in size.

4. The *M. trapezius* is attached to the outer fifth of the clavicle, and is therefore widely separated here from the *M. sterno-mastoideus*. Beneath the acromial part of the muscle, a second and thicker stratum passes upwards to the cervical vertebrae (*M. acromio-trachelianus*). Similarly, a *M. occipito-scapularis* blends with the rhomboid sheet, which is thus carried up to the skull. Lastly the *M. levator anguli scapulae* may be found in continuity with the *M. serratus magnus*. Such muscles provide useful stays for the fixation of the shoulder in climbing movements.

The *M. deltoideus* occupies the whole of the ventral surface of the clavicle (no clavicular component of the *M. pectoralis major* being developed). This muscle will be found to extend also along the whole length of the scapular spine as far as the vertebral border of the bone.

The *M. pectoralis major* is thus "sternal" only in origin: but its presternal component is now of considerable size. The *M. pectoralis minor* arises likewise from the sternum (not from the ribs) and it is inserted into a fascial sheet laid on the coracoid process, but not strongly attached thereto. A third pectoral muscle (possibly fused in Man with the great pectoral muscle) arises from the lower costal cartilages, and passes alongside the lesser pectoral mass into a fascial expansion over the shoulder-joint. The subclavius muscle is distinct or large. The *M. latissimus dorsi* is characterized by its accessory, viz. the *M. dorsi-epitrochlearis* or *M. latissimo-condyloideus*, seen in the Lemurs and Tarsius. The

M. latissimus remains devoid of tendon fibres till near the humerus. It has no scapular component, and its most anterior (cephalad) fibres pass behind the tendon of the *M. teres major* (Kohlbrugge¹ has referred to this), of which muscle these fibres may form an aberrant portion.

5. The *M. biceps humeri* is not provided with a *lacertus fibrosus*. The *M. coraco-brachialis* is subdivided into longer and shorter components.

6. The muscles of the thumb present no essential differences from those of the Lemur (*v. p. 79 supra*). Each of the other digits is provided with two extensor tendons, a deep tendon being added to that of the *extensor communis* in each instance.

7. The crura of the diaphragm may extend caudally as far as the fourth lumbar vertebra (in *Semnopithecus*, cf. Kohlbrugge). The muscle is thin and its central tendon less extensive than in the Lemur. "Arcuate ligaments" are not distinct, the muscle-fibres arising locally from the fascial sheath of the *M. quadratus lumborum*.

8. The *M. gluteus maximus* is small: it arises however from the caudal as well as the sacral vertebrae, the caudal part forming a separate caudo-femoral muscle: the femoral attachment is greatly restricted in extent: the rest of the muscle joins the *M. tensor fasciae femoris* and thus is continuous with the ilio-tibial band. The latter is not distinctly specialized and the fascial sheet by which it is represented expands generally above the patella and round the front of the knee-joint. The small separable deep component of the *M. gluteus minimus*, known as the *M. scanorius*, is usually present (Kohlbrugge). The *M. biceps femoris* possesses but a single head (the "long" head of human anatomy) which merges into the fascia covering of the muscles on the anterior aspect of the leg. Thus it comes to be attached to the tibia. The New-World monkeys possess the short or femoral head of this muscle, as described by Professors Windle and Parsons (*Proc. Anat. Soc.*, Nov. 1899). The short head of the muscle is identified² by those authors with the *M. tenuissimus* (Parsons)

¹ *Muskeln und Nerven der Primaten*, Amsterdam, 1897, p. 69.

² This identification was confirmed independently three years later by Klaatsch, whose strictures on the lack of perception of his anatomical colleagues in this country provide amusing reading in view of the facts as to priority in this matter [cf. *Morphologisches Jahrbuch*, Band xxix. 1902, especially pp. 219, 221].

found in some of the lower Eutheria. But even the *M. tenuissimus* is not known to exist in the Cercopithecidae.

The adductor mass of femoral muscles is well developed. The *M. adductor longus* is large and contains few tendinous fibres. The *M. adductor brevis* is only to be separated artificially from the *M. adductor magnus*. The latter is clearly composed of two elements, and the superficial artery passes between them obliquely as it enters the popliteal space. One part of the muscle (supplied by the sciatic nerve) arises close to the tuber ischii and ends at the medial condyle of the femur (pars ischio-condylaris). The remainder (supplied by the obturator nerve), arising from the rami of the ischium and pubis, is inserted into the femoral shaft, and extends over the "popliteal area" of that bone.

The *M. gracilis* is wide and strong. Below the knee-joint it is inserted partly into the tibia (entirely so in the Semnopithecidae: Kohlbrugge), and partly into the deep fascia of the leg. The tendon of the *M. semitendinosus* has a similar (twofold) distribution.

The *M. quadriceps extensor cruris* consists of the usual components. The *M. rectus* has a large flattened "acetabular" head (the "reflected" head of human anatomy), while the second head is distinct though small in *Cynocephalus*. The *M. vastus lateralis* is more extensive about the great trochanter than is the *M. vastus medialis*. The *M. vastus intermedius* is closely related to the latter, and gives off no fibres (save possibly a few to its lateral side) to form a *M. subcrureus*.

As in the Lemur, the *M. soleus* in the Cercopithecidae owns a fibular origin only. The *M. plantaris* sends a long slender tendon downwards between the *Mm. gastrocnemii* and soleus. This tendon is intimately connected with the tendo Achillis. Yet it can be dissected away from this, without much difficulty. Then it will be found to pass round the heel to become continuous with the plantar fascia. The muscle is reduced in size as compared with that of the Lemur (and of *Tarsius*¹).

(i) The chief features of the plantar fascia consist (according to Loth²) in the marked development of the "aponeurosis tibialis"

¹ v. the illustrations in Vallois' memoir on *Platycnemia*, *Bulletin de la Soc. d'Anth. de Paris*, 1912, p. 274.

² *Correspondenzblatt der Deutschen Anth. Ges.* xxxviii. 1907.

(a sheet of fibres not found in the true Lemurs). The fibular part of the aponeurosis becomes attached deeply in the region of the fifth metacarpal bone (proximal part). A deeply-placed intermediate aponeurosis runs towards the first digit, but the original "fasciculus hallucis" (seen in Lemurs) does not reappear. The outstanding point is the strengthening of the middle parts of the aponeurosis, and this feature is directly related to the environment of the animals concerned, for it is greatest in those, such as *Cynocephalus hamadryas*, of terrestrial rather than purely arboreal habits.

(ii) The *M. flexor brevis digitorum* arises partly from the plantar fascia. In a young male *Cynocephalus mormon*, I found an arrangement identical with that represented by Dr Sawalischin¹. Thus the superficial head (derived from the plantar fascia) furnished a tendon to the second digit, and an indefinite fascial expansion directed towards but failing to reach the third digit. The deep head arose from the tendon of the *M. flexor longus digitorum* (flexor tibialis) and provided perforated tendons for the third, fourth and fifth digits.

(iii) The *M. flexor longus digitorum* supplies the four outer digits and is joined by a *M. flexor accessorius* which has but one head of origin.

(iv) *M. flexor hallucis longus* (flexor fibularis) is conjoined with the tendon of the preceding muscle, and contributes tendons to the hallux and three next digits, but not to the fifth toe.

While the conditions in general resemble those already noted in the Lemur, a few points of distinction may yet be found. Thus the differences are least in the upper limb, and here no functional divergence of note has occurred. In the lower limb, the monkey shews signs of a tendency to emancipate this organ from a solely arboreal function. The strengthening and increased rigidity of the plantar fascia, the development of a *M. flexor accessorius*, and the withdrawal of part of the *M. flexor fibularis* (from the fifth toe) together with the relative shortening of the digits, all point to an increased adaptation of the foot to a truly plantigrade (as contrasted with a prehensile) function.

A muscle in the orbital cavity named *M. choanoides* (or *M.*

¹ *Morphologisches Jahrbuch*, Band XLII. Heft 4, S. 598, Fig. 20b.

retractor bulbi oculi) is found constantly in the Cercopithecidae. It is unknown in the New-World monkeys¹, in the Simiidae, in Man², and Burmeister neither mentions it, nor does he figure it in Tarsius. So irregular a distribution must own some definite significance, but as yet this is obscure.

G. Vascular System. The heart is placed mesially³, but the apex has just reached the left side of the sternum (in Cynocephalous monkeys it may retain the mesial position) where it lies close to the sixth costal cartilage. The form of the heart also shews an advance on that of the Lemurs, for the transverse diameter begins to assert a superiority over the dorsi-ventral one. Again the long axis of the heart is more strongly inclined to that of the post-caval vein, and therefore is pointed less directly towards the diaphragm. The intra-thoracic course of the post-caval vein is correspondingly shortened but is still distinct; the subpericardial sinus (with the lobus impar) still persists, while a "bursa infracardiaca" of "peritoneal" origin has been seen in Cynocephalus by Professor Peter Thompson. The diaphragmatic contact-area of the pericardium is however enlarged. The great vessels sometimes arise from the aortic arch as in Man. More commonly, however, only two trunks arise thus. Of these the first or innominate gives origin to the left common carotid artery and then bifurcates as in Man. These characters may be taken to indicate the early stages of a thoracic enlargement, and a change in form related to the shortening of the torso, and presumably adapted to the assumption of the erect attitude.

The axillary artery still retains a primitive arrangement by providing a large subscapular trunk for the circumflex arteries of the humerus and scapula. But the A. circumflexa humeri anterior tends to be detached from this and to arise independently from the axillary vessel. Herein the Cercopithecidae (especially Cynocephalus) approach Man more closely than do the Simiidae. The brachial vessel is almost always of the "superficial" type, crossing the median nerve superficially,

¹ Ottery, *P. Z. S.* 1879, p. 127.

² Except as an anomaly: cf. Mr Whitnall's specimen, *J.A.P.*, xlvi. Oct. 1911, p. 36.

³ Ruge, *Morph. Jahrb.* Bd. xix.

and dividing usually above the level of the elbow joint. Thus various types of the "high origin" of the radial and ulnar offshoots are produced, and the arrangements are similar to those found in many human fetuses before the end of the sixth month of intra-uterine life. The radial and ulnar contributions to the palmar arches are about equal in size in *Cercopithecus*, while in the *Cynocephalous* monkeys the ulnar artery is the smaller of the two and thus more primitive. In the lower limb, the deep branch of the common femoral artery is less developed, i.e. it gives off fewer important branches than in Man. In particular the *A. circumflexa medialis* may arise (with the *A. obturatoria*) from the *A. hypogastrica*. A distinctive feature is the *A. saphena* which runs from the thigh to the foot in a subcutaneous situation, and ends mainly as a vessel perforating the second interosseous (metatarsal) space. The *A. poplitea* is not pressed into the fold of the knee (as in Man), and its position like that of the *A. saphena* seems to be determined by the characteristic flexure of that joint. The two plantar arteries are present, but small, the chief supply to this part coming *via* the *A. saphena* through the second space as described above.

H. Nervous System. i. The *Cercopithecidae* possess a brain conspicuous for certain details of specialization.

Foremost among these, the large size of the corpus callosum may be mentioned. This character is not only expressive of the increased mass of the neopallium, but it indicates particularly an augmentation of the association areas of the cortex. The extension of the latter is the more important character. But the boundaries and extent of those areas are not evident until a variety of details have been studied. The corpus callosum is easily exposed to view, and since its limits are distinct, it has been placed in the foreground here.

The cerebellum has also increased in relative bulk and is nearly as instructive as the preceding characters.

ii. Examples of conditions apparently primitive, but with better reason ascribed to degenerative changes, are insignificant or absent. Where degeneration has taken place its effects are not of this kind.

iii. The Cercopithecidae maintain the high development of the visual sense noticed previously in the Lemurs and Tarsius. Consequently it is not surprising to find that the form of the cerebrum is strongly influenced by the necessity of providing the requisite mechanism.

iv. The neopallium is not in all cases very highly convoluted, and consequently the statement regarding the exuberance of its development might seem to be controverted hereby. The relatively small size of most of the animals under consideration must evidently be taken into account when this objection is raised. If this be done no appreciable discrepancy of statements remains.

Some additional details may now be added. The Anthroipoidea are microsmatic¹, the Cercopithecidae providing no exceptions to this rule. Thus the olfactory bulb is reduced in size, while its tract is pedunculated, i.e. elongated and attenuated in a marked degree. The tuberculum olfactorium is still recognizable, and a remnant of the fissura rhinalis appears as the incisura temporalis (cf. Fig. 84). But the olfactory commissures, i.e. the anterior commissure and the psalterium, together with the fornix, are greatly reduced in relative bulk. The marginal pallium presents no features deserving special comment.

The large size of the neopallium has been remarked already. The occipital end of the hemisphere overlaps the cerebellum (most extensively in the small American monkeys, *Chrysotrrix* and *Hapale*). This part of the cortex (the area striata) has peculiar histological features, wherein the Cercopithecidae are approached by Tarsius, while they stand in contrast to the Lemurs.

The occipital pole of the neopallium contains an extensive posterior cornu of the lateral ventricle of the brain, providing thus the material for comment similar to that just passed on the area striata.

The plan of the neopallial convolutions is presented in the accompanying illustrations (Figs. 85, 86). The presence of an "insula" in the lower part of the Sylvian fissure demands special notice, as indicative of the local growth of the surrounding parts. The extent of the frontal, parietal, and temporal association areas is shewn in Fig. 85, with which the corresponding diagrams for

¹ Cf. references to literature on p. 43.

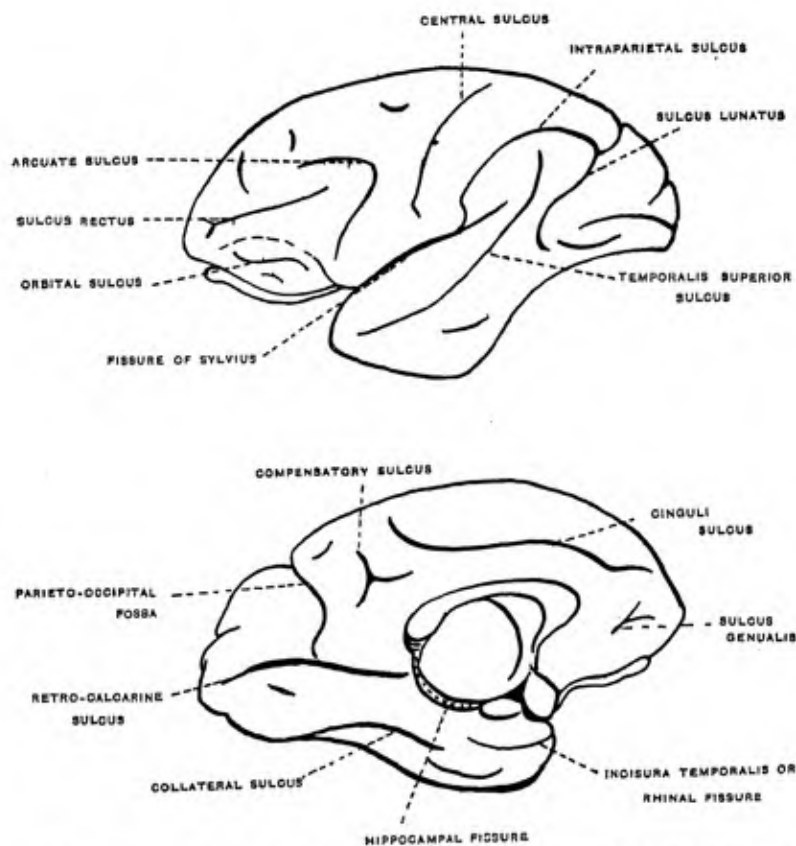


Fig. 84. The left cerebral hemisphere of a Semnopithecus monkey (Cercopithecidae). The main features are similar to those of the human brain: on the mesial aspect the small post-splenial gyrus A. Retzii is not visible, and the fascia dentata has not been exposed.

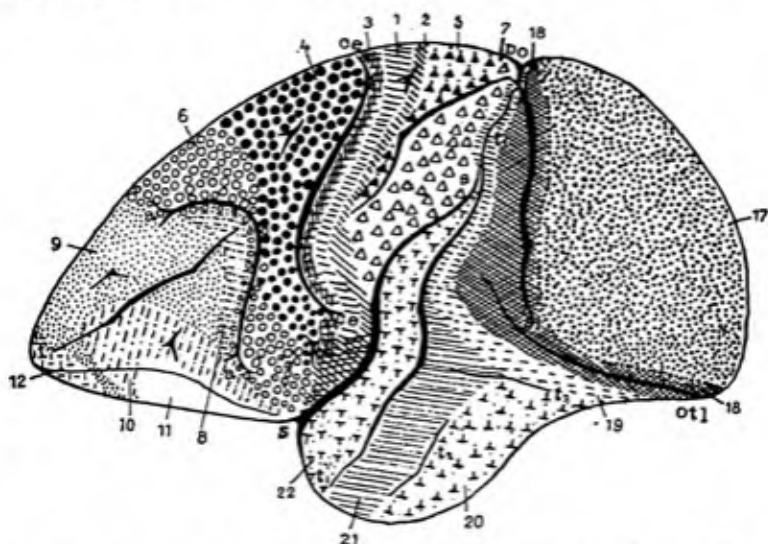


Fig. 85. *Macacus* sp.? Cortical areas of the brain. Lateral convexity. (From Brodmann, *op. cit.*) Note specially the areas marked 1, 4, and 17, and compare with Figs. 46 and 64.

- No. 1. Area post-centralis (sensory).
 No. 4. Area giganto-pyramidalis (motor).
 No. 17. Area striata (visual).

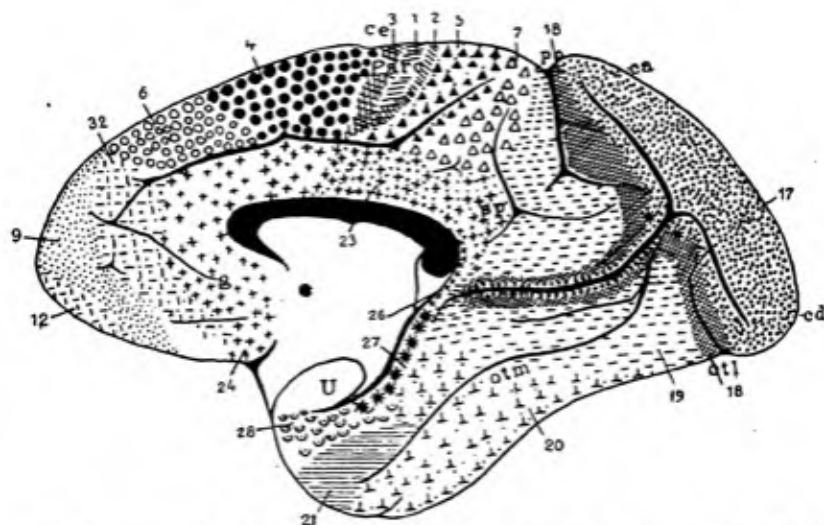


Fig. 86. *Macacus* sp.? Cortical areas of the brain. Mesial aspect of hemisphere. (From Brodmann, *op. cit.*)

Hapale (Fig. 87), the Lemur (Fig. 46) and Tarsius (Fig. 64) are to be compared.

The mid-brain has undergone little or no evolutionary change. The cerebellum is enlarged as compared with its condition in the Lemurs. Its form is modified by the contact of the occipital lobes.

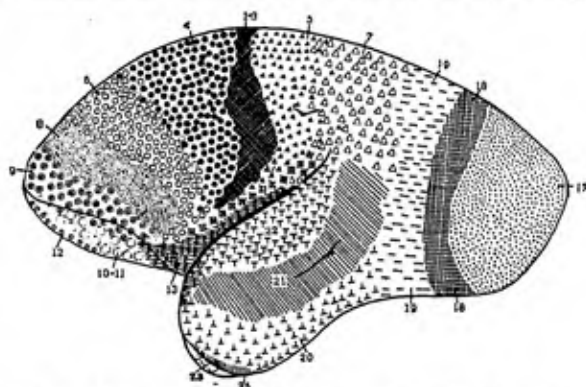


Fig. 87. *Hapale jacchus*, a small American monkey (Marmoset). Cortical areas of the brain. Lateral convexity. For comparison with Figs. 46, 64, and 85. (From Brodmann, *op. cit.*)

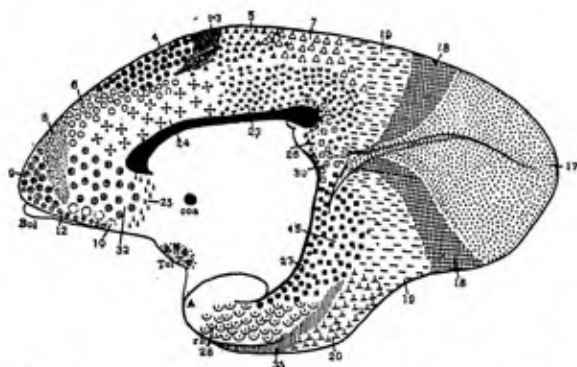


Fig. 88. *Hapale jacchus*. Cortical areas of the brain. Mesial aspect of the hemisphere. For comparison with Figs. 47 and 86. (From Brodmann, *op. cit.*)

The floccular lobe is still divisible into a flocculus and a paraflocculus. Both are reduced in size, but the paraflocculus retains a petrosal lobule which the Cercopithecidae possess in common with some more lowly mammals. The pons varolii is large, but the trapezium is still exposed on the surface along its hinder margin.

In studying the peripheral nerves of the Cercopithecidae, we encounter again evidence (as in the Lemurs) of a tendency to the mode of the limb-plexuses to be "post-fixed" as compared with the usual human type. [When comparable nerves in two plexuses do not leave the cord at the same level, the plexus in which this level is further from the brain is "post-fixed" as contrasted with the other.] The tendency mentioned above will be realized best by considering some actual results of dissections.

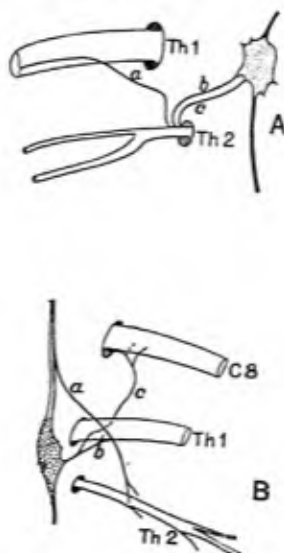


Fig. 89. Communications between the upper thoracic nerves and the Sympathetic cord in (A) *Cynocephalus mormon*, a representative of the Cercopithecidae, and (B) a Lemur. In (A), the second thoracic nerve (Th2) is seen to divide, and the upper branch of division joins the Brachial plexus. (From dissections by W. L. H. D.)

The brachial plexus in a series of primate animals has provided information which may be tabulated as follows:

Plexus brachialis.

I. *Nervus axillaris*: Segmental derivation in terms of cervical nerves.

Man : C₅ (or C₄, C₅). (Harris¹.)

Cercopithecidae: C₅, C₇. (Kohlbrugge²)
(and Lemurs).

¹ J. A. P., July, 1904.

² Kon. Ak. van Wet. Amsterdam, 1897.

II. Contribution from the second thoracic nerve.

Man: variable, and usually small.

Cercopithecidae: variable but often large (cf. Fig. 89).

From these data (I and II), it appears that the plexus in the Cercopithecidae tends to a position more distal than that of Man.

A similar conclusion will be drawn from the study of the lumbar or of the sacral plexus in the several forms. Here it will suffice to record the evidence of the N. femoralis (anterior crural nerve).

<i>Nervus femoralis</i> :	Segmental derivation in terms of thoraco-lumbar nerves
Man:	14, 15, 16. (Quain ¹ .)
Cercopithecidae:	... 15, 16, 17, or 16, 17, 18. (Kohlbrugge ² .)
Tarsius:	... 15, 16, 17. (Ruge ³ .)
Lemur: 17, 18. („)
Tupaia (an insectivore): 17, 18. (Leche ⁴ .)

In the lumbar plexus, the process of reduction in the number of thoraco-lumbar vertebrae is doubtless influential so far as Man is concerned, but this factor must be excluded in the case of the brachial plexus. An appeal to modifications induced by the erect attitude has been deemed reasonable if not sufficient, but of late, objections have been brought against this explanation by Professor Wingate Todd.

However this may be, the various members of the Primates fall into a sequence when judged by the test as applied to the lumbar plexus, and the sequence is identical with that considered on a summary of the whole evidence to be the natural one.

Before passing from the nervous system, it should be added that the Cercopithecidae (or at least those in which the tail is long) agree with other long-tailed mammals in the possession of well-marked coccygeal or caudal nerves concentrated in a long "collector" nerve on each side of the tail.

¹ Quoted by Kohlbrugge, *op. cit.*

² *op. cit.*, cf. p. 143 *supra*.

³ *Morphologisches Jahrbuch.*, Band XVIII.

⁴ Quoted by Ruge, *op. cit.*

I. Respiratory System: the Larynx. The hyoid bone is characterized by the enlargement and downward extension of the basi-hyal. The latter however is not excavated in the Cercopithecidae as in the Cebian Mycetes (Howling Monkey). The laryngeal apparatus generally resembles that of Man, all the muscles and cartilages of the human larynx being recognizable. Coronal sections of the larynx reveal one or two distinctive features (cf. Fig. 90).

Most obvious perhaps is the relatively long and thin plica vocalis. The unusual extent of the *M. crico-thyroideus* on the deep aspect of the thyroid cartilage is also evident.

The Lungs. The lungs are more subdivided than in Man; in the left lung (Fig. 92) there are three lobes corresponding in a general way to the three lobes normally found in the right human lung. In the right lung (Fig. 91) the three lobes (of human anatomy) will be found supplemented by a fourth lobe; this lobe, which is small and pendulous, is known as the lobus impar: it is situated beneath the right bronchus and sometimes it sends a process leftwards crossing the oesophagus anteriorly and thus encroaching on the posterior mediastinum and left side of the thorax. This involves a modification of the right pleural membrane, and the production of a diverticulum to contain the lobus impar. The diverticulum is called the sinus subpericardiacus¹, and its passage between the oesophagus and the post-caval vein beneath the pericardial sac is doubtless related to the limited attachment of the latter to the diaphragm.

The pleura may form a cervical dome in rare instances among the Cercopithecidae, but such cases are exceptional² in these animals and absent from other Primates. Behind the sternum the first contact of the two sacs is nearer the head than in Man, and the sacs accompany each other further before they diverge. The left pleura first breaks away over the pericardium, but the uncovered area of the latter is relatively small in extent. The pleural sacs extend far down the vertebral column behind, in Cercopithecidae reaching to the vertebra below the last thoracic.

¹ Ruge, *Morphologisches Jahrbuch*. The Lemur possesses a lobus impar and the corresponding pleural pouch.

² Patten, *op. cit.*, 1899, p. 10.

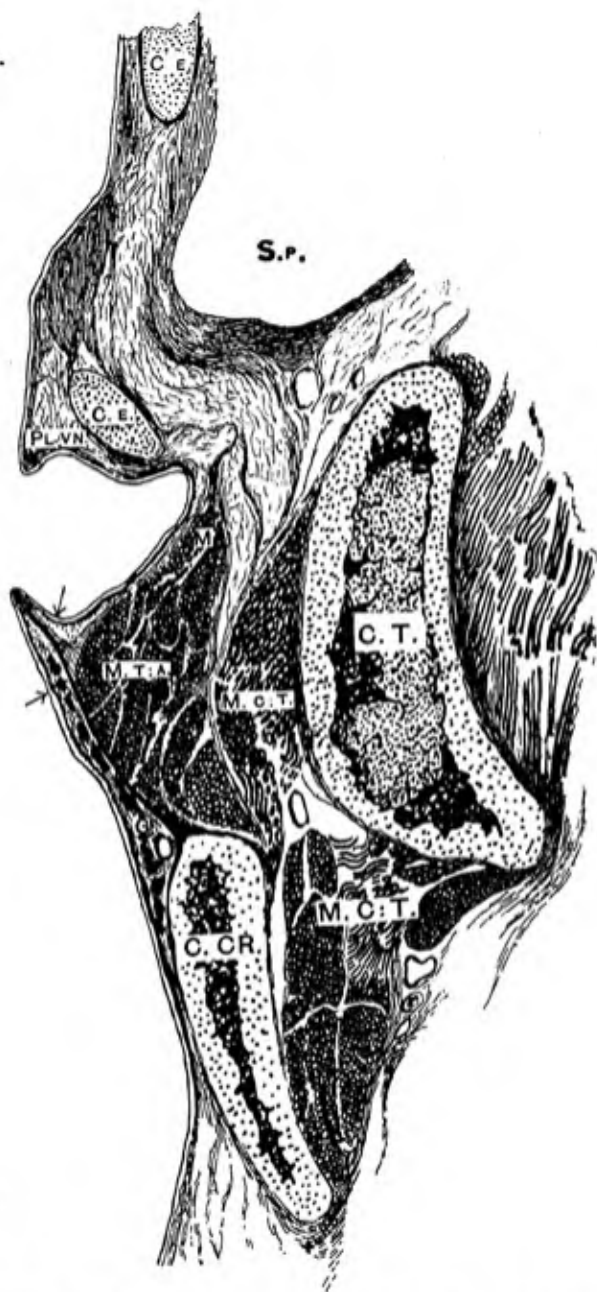


Fig. 90. *Macacus nemestrinus* (adult male). Coronal section of middle portion of plica vocalis. No muscle-fibres in plica ventricularis. Note the upward extent of the *M. crico-thyroideus* internally to the thyroid cartilage. There is an indication of stratified epithelium on the surface of the plica ventricularis. ($\times 8.1$.)

The latter may be the fourteenth thoracic in these animals. Thymic remains are visible on the anterior aspect of the pericardium, which is also crossed by the right phrenic nerve.

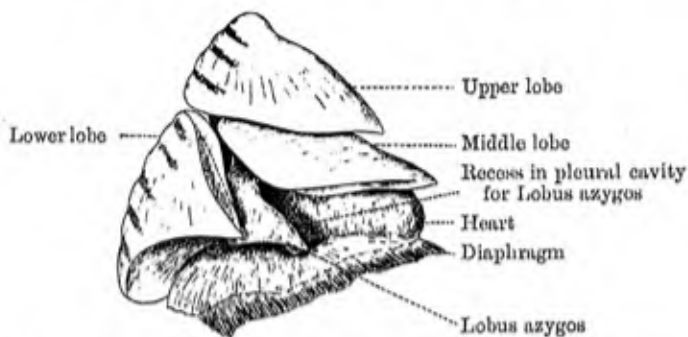


Fig. 91. Lateral aspect of the right lung of a Cercopithecus monkey (Cercopithecidae) to shew the lobus azygos impar.

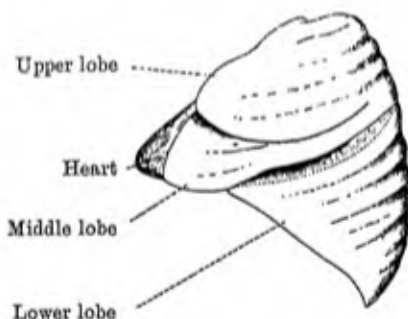


Fig. 92. Lateral aspect of the left lung of a Cercopithecus monkey (Cercopithecidae). The heart is also shewn. The lung is divided into three lobes, thus differing from the human lung of the left side, while resembling the right human lung.

J. Alimentary System. Sections of the lips of a Cynocephalous monkey (Fig. 93) shew that the *M. orbicularis oris* is met with in cross-section, and extends thus as an attenuated band to the free margin of the lip, where it is slightly recurved. Mucous glands are abundant here, as also around the entrance to the cheek-pouch. The *M. buccinator* is spread out over the wall of the latter and indeed is pulled downwards as it follows the neck

of the pouch. Superficially to the *M. buccinator* may be seen another cutaneous muscular stratum, representing part of the platysma sheet.

In correspondence with the proportions of the maxillary and mandibular skeleton, the tongue is elongated and presents almost a truncated appearance anteriorly. The tonsils are small. The oesophagus has much the appearance and relations presented by the corresponding human structure, and on its way to the stomach it grooves deeply the posterior aspect of the left lobe of the liver. The latter organ is a simple sac, but in one genus, viz. *Semnopithecus*¹, the stomach is extraordinarily sacculated.



Fig. 93. Sections of upper and lower lip. *Cynocephalus*, ? . (? Sp.)

This peculiarity occurs in the Asiatic *Semnopithecus*, and the African *Colobi*, being less exaggerated in the latter. Other characters (ex. gr. diminution or absence of cheek-pouches, and excess in length of the hinder limbs over the fore-limbs) are associated with this modification of the stomach, which may be attributed provisionally to the largely vegetarian diet of the animals possessing it.

The distinctive features seen in an adult *Semnopithecus* (*Nasalis*) are shewn in Fig. 94. The enormous stomach dwarfs the thoracic viscera in size, and it has displaced the liver completely from the left hypochondrium and the epigastric region. The liver is modified to an extent rendering it unrecognizable as that of a primate mammal. The spleen has been greatly displaced and is likewise of peculiar form.

These profound changes are attributable (as suggested above) to the particular diet of these monkeys. This idea is the outcome of observations on the modifications of the stomach in herbivorous mammals of other Orders. But Schwalbe² reasonably suggests that the stomach in *Semnopithecus* is also capable of providing for rumination. If such be the case, the ultimate factor is still a physiological one. And the importance of bearing in mind the influence of physiological factors is again impressed on the student of morphology. Another important reflexion is that the skeleton does not enable us to predict the discovery of such aberrations of the morphological dispositions as we actually find in the perishable viscera here described.

¹ The name *Presbytis* replaces *Semnopithecus* in the latest nomenclature.

² *Z. f. A. u. M.* 1912, Sonderheft II.

Lastly the occasional though anomalous occurrence of a stomach of Semnopithecine form in adult human beings is not unknown. Such an instance has been recorded by Melsome¹. More striking even than this, however, are the examples described by Professor Schwalbe², who has confirmed and extended the observations of Professor Keith and Dr Wood-Jones³ on the form of the human foetal stomach.

These observers have shewn that the human foetus from the third to the fifth month of intra-uterine life possesses a remarkable diverticulum at the cardiac end of the stomach. Later in development this diverticulum dis-



Fig. 94. Viscera of a *Nasalis* monkey (*Cercopithecidae*): the extraordinarily modified form of the stomach and the consequent displacement of the liver to the right are to be noticed. These features are found throughout the genus *Semnopithecus*, which includes many species of monkeys found in Asia. (Cf. Fig. 22.)

1, Stomach; 2, Liver; 3, Pancreas; 4, Spleen; 5, Duodenum; 6, Caecum.

appears, but while present, it is lined with a specially corrugated mucous membrane. Observations on the stomachs of foetal *Semnopithecus* shew that the peculiar modification found in the adult organ consists in a dilatation of the fundus (or as Schwalbe suggests, the cupola) which incorporates the diverticulum. A second division of the stomach called *Tubus gastricus* is

¹ *Proc. Anat. Soc.*, May 1895.

² *Z. f. A. u. M.* 1912, Sonderheft II.

³ *Proc. Anat. Soc.*, Nov. 1901.

found to be sacculated in the human foetus (at the period mentioned above) in a fashion similar even in details to that met with in the adult *Semnopithecus*. The most important inference to be drawn from all this, is that the "simplicity" of the human stomach is secondary and not primitive. This subject will be considered further in the sequel. To return to the *Semnopithecus*, I may add that in a foetus or very young specimen (examined by me) having a rectilinear length of 160 mm. from vertex to coccyx, the liver still covers the stomach extensively. But the dilatation is already pronounced and a series of foetal specimens would doubtless demonstrate the whole process of the displacement of the liver and the curious scroll-like deformation undergone by that organ. In an adult *Semnopithecus* (*Nasalis*) the liver has been pressed so far rightwards that it appears actually fused with the diaphragm. Yet this unusual relation is shown by the foetal example to be secondary.

A well-developed omentum resembling that of Man, extends downwards over the small intestine, and may be traced to the ascending colon as well as the transverse colon (to which it is limited in the higher types). The small intestine has the same general relations as in Man, being provided with a mesentery, distinct even in the duodenal portion of the gut. The caecum is bluntly pointed, a vermiform appendix failing to develop. The ascending meso-colon should be noticed, and the meso-rectum is distinct and extensive, this part (the rectum) being characteristically straight.

The liver (Fig. 95) still presents (a) quadrupedal or pronograde features, but nevertheless it differs from that of the Lemur in certain respects. (b) The peritoneal attachment to the diaphragm and posterior abdominal wall is still "linear," the "bare area" (characteristic of higher types) not having yet appeared. (c) The incisura oesophagea is variable in form in different genera. In the Cercopithecini it is deep and therefore more primitive, but in the Cynocephali (and in certain New-World monkeys) it is shallow. Thus the shallow stage may be attained by a particular form in widely separated groups ex. gr. in *Tarsius* as contrasted with the Lemuroidea, and in *Cynocephalus* as contrasted with the other Cercopithecidae. It recurs in all the highest Anthropoidea including Man. This phenomenon (viz. the repetition of the attainment of a certain conformation, or a detail of structure, in a series of animals capable of

arrangement in an evolutionary sequence), is worthy of much consideration¹.

Some distinctive features of the liver may now be enumerated. Thus (*a'*) the incisura duodenalis is filled up and obliterated; (*b'*) the left lateral lobe is withdrawn from the right side of the abdomen, and with its decrease, the preponderance of the right

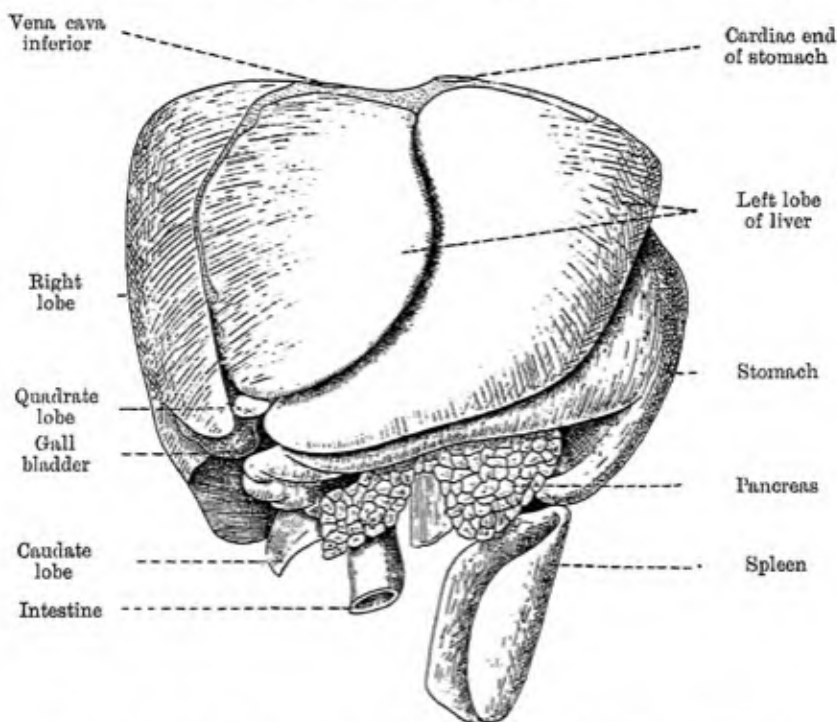


Fig. 95. Liver, Stomach, Pancreas and Spleen of a *Cercopithecus* monkey.

side of the liver is seen to begin; (*c'*) the true lobus caudatus is no longer falciform; it is almost wholly ventral to the post-caval vein, the leftward position (seen in Lemurs) having been

¹ Ruge has pointed out that this is true for the apparent shortening of the trunk (cf. *Morph. Jahrb.* Bd. xix. S. 249). The same writer (*Morph. Jahrb.* Bd. 35) remarks on the recurring evidence of the lowly position of the genus *Cercopithecus*, adding that they are separated from the *Cynocephali* and others of the *Cercopithecidae* by a wide interval not bridged by any living genus. These remarks are based on the study of the liver.

abandoned; (*d'*) the right lateral lobe has reduced its contact-area on the lateral aspect of the right kidney; (*e'*) a prominence of the left lobe called "processus triangularis" now appears; it is lost again in Man, or is represented only by the tuber omentale, save in anomalous instances.

The pancreas and spleen have relations similar to those seen in Man. But the spleen of *Cercopithecus* (if the stomach be not distended) may come into contact with the liver owing to the persistently large size of the left lobe of the latter organ.

Genito-urinary System. In a young specimen of a *Cephalopterus* monkey (*Cercopithecidae*) the right kidney is situated posteriorly (*i.e.* caudally) to the left; the right suprarenal body is elongated and nearly cylindrical, the left being pyramidal in form. The anterior renal surface is much more convex than the posterior surface. Into the renal pelvis a single pyramid bulges distinctly, though there are indications that a series of sections might reveal more than one such protrusion. The genitalia are considered in the two sexes separately.

A. The male. The testes in the foregoing example are still situated in the inguinal canal, though close to the "external ring"; it will be noted that the specimen though admittedly young, nevertheless having acquired the first permanent teeth, corresponds in age to human children of six to seven years.

The penis is protected by an elongated prepuce attached far behind the glans, a fraenum praeputii being entirely absent. The long penile urethra is supported by the cartilaginous "os" penis, and terminates posteriorly in a distinct bulb, the latter being well protected by the concrescence of the two ischial callosities in the middle line of the perinaeum. The prostate gland is large, unilobular, and firmly attached to the rectum as well as to the urethra and base of the bladder.

The membranous urethra contains a distinct spheroidal caput gallinaginis with lateral depressions.

The abdominal peritoneum is reflected almost horizontally forward from the fundus of the distended bladder.

B. The female. The genitalia of a young female *Cynocephalus mormon* provide material for the following notes. Externally, the

clitoris is so large as to constitute a penile appendage, which however is imperforate, the urethral aperture being independent of this organ. The prepuce is long and hood-like, cleft inferiorly, and it covers a distinct and bifid glans with crura and corpora cavernosa. Like the body of this female penis however, the glans is imperforate. The former is grooved posteriorly and the urethral orifice (meatus urinarius) is still more posteriorly situated. The vagina is proportionately long and straight, without a hymen: its walls are thrown into longitudinal folds, most distinct on the posterior aspect.

The pouch of Douglas is shallow, and the rectum descends almost vertically behind the uterus and vagina. No special description of the uterus, tubes, ovaries, uterine and ovarian ligaments, or bladder is called for in view of their close resemblance to the corresponding parts in the Hominidae.

The sperm-cells in *Macacus* and *Cynocephalus* have been described by Professor Retzius. The cells are larger in those animals than in *Lenur catta*, and in fact surpass all others, those of the Orang-utan alone excepted. In the Cercopithecidae, it would thus appear that the head is of a broad ovoid form (cf. Fig. 51, No. 2) distinctly flattened in one plane. The acrosome is not clearly distinguishable from the nuclear portion. The pars conjunctionis (Verbindungsstück) is shorter than in the Lemur, but longer than in the Simiidae and Man. Of the tail, the pars principalis (Hauptstück) is very long, while the pars terminalis is relatively short.

(ii) *Anthropoidea* (continued).

Simiidae. As noted in the chapter on Classification, the family Simiidae includes the four groups represented by the Gibbon (*Hylobates*), Orang-utan (*Simia*), Chimpanzee (*Anthropopithecus niger*) and Gorilla (*Anthropopithecus gorilla*)¹. The first two

¹ The question of synonyms has long been a vexed one. Those given above are retained because it is thought that they are the most widely known. The latest proposals for a scientific nomenclature which shall take priority into account, are set forth by Lord Rothschild, F.Z.S., in *Novitates Zoologicae*, 1908. Therein the distinctive names (for the three larger forms) are Pongo (Orang-utan), Simia (Chimpanzee), and Gorilla.

are found in Asia, the two latter in Africa, and all are tropical, though the Gibbons extend into the northern sub-tropical region.

In the following paragraphs, the Gorilla will be described as the representative of the family, but so divergent in many ways are the members of the latter, that references to each in turn will be needed. No single member can be regarded as typical of the whole series, and much stress is laid on this point. In such a work as this, the exigences of space preclude detailed descrip-



Fig. 96. *Hylobates mulleri*. (From a group in the Lübeck Museum.)

tions of each form, and partial accounts are now readily accessible elsewhere. It remains to give reasons for the choice of Gorilla. *Hylobates* (Fig. 96) is set aside because it is still reminiscent (so to speak) of the *Cercopithecidae*, though in some respects highly developed. The Orang-utan (Figs. 97, 98) is the visible expression of Nature's scorn for those morphologists who ignore physiological considerations. In more definite terms, it presents a complex assortment of adaptive, progressive and even degenerate characters.



Fig. 97. A young Orang-utan. (From a specimen photographed in Sarawak, Borneo, by Dr C. Hose.) The attitude suggests strongly the adaptation of the Orang-utan to an arboreal mode of existence.

The Chimpanzee and Gorilla remain. On purely morphological grounds, the Chimpanzee ranks second of the two. For the moment, these grounds must determine the choice, and the Gorilla will be selected as presenting an anatomical constitution indicative that the arboreal habitat has been more completely abandoned than in the other Simiidae. The conformation of the brain places it above the Chimpanzee, even though the latter should seem



Fig. 98. Head of a large male Orang-utan. The physiognomy is to be compared with that of the Gorilla (Fig. 99). (From a specimen presented to the Cambridge Collection by Dr C. Hose.)

more tolerant of captivity and more capable of domestication or even education¹.

The Gorilla is an inhabitant of tropical Africa, and though it is not exclusively arboreal, yet the younger and smaller individuals

¹ Though less amiable the Gorilla may be possibly as intelligent as the Chimpanzee: a young specimen (Mus. Anat. Cant. H) lived for a few weeks in captivity, and shewed itself to be as docile and tractable as a Chimpanzee. Similar observations have been made in Africa. No adult male Gorilla has yet been captured alive. It is also noteworthy that young Gorillas and Chimpanzees alike are extremely liable to disease in captivity even if kept in their natural geographical situation in West Africa.

are largely so, and in all cases the animal frequents woodlands. The Gorilla is the largest of the Simiidae, and the adult male is the heaviest Primate mammal, surpassing even the Hominidae. Estimates of the stature of Gorillas are not usually reliable, but



Fig. 99. An adult male Gorilla from the Sangha District, W. Africa.
(With permission.)

there is no doubt that several varieties exist, and these are distinguished (to some extent at least) in point of size. The status of these varieties opens up an interesting but not a simple problem, viz. how far they represent local species, or variants more properly

styled sub-species. (The problem is identical with that of the taxonomic description of the several Races of Mankind.) A recent writer (Rothschild, *op. cit.*, v. p. 153 *supra*), adopts a trinomial mode of classification, and recognizes a single genus and species of Gorilla with five sub-species¹.

A. General External Characters². The preceding illustration (Fig. 99) will furnish a better idea of the general appearance of an adult male Gorilla than could be conveyed by many lines of text. A noteworthy feature is the span of the arms, which often exceeds eight feet. The animal has retained here at least one "arboreal" character. On level ground, the Gorilla moves in a crouching attitude, using the arms somewhat like crutches. The fingers are then bent and the skin on the dorsal aspect of the terminal joints becomes thick and callous. (In the longer-armed Orang-utan, the whole length of the fingers as far as the knuckles, is applied to the ground.) The thumbs are small and feeble; the great toe on the contrary very powerful, though shorter than the other toes (*cf.* Fig. 100), which are usually "webbed." The latter phenomenon may also be regarded



Fig. 100. Hand and foot of adult male Gorilla.

¹ The names are as follows.

1. *Gorilla gorilla gina*.
2. " " *manyema*.
3. " " *matschiei*.
4. " " *diehli*.
5. " " *beringeri*.

Probably other sub-species may be discovered. There is no doubt that individuals often exceed the average dimensions so much as to be veritable "giant-forms" of Gorilla.

Lord Rothschild recognizes five *species* of Chimpanzee, and one species of Orang-utan with at least four sub-species. The Gibbons (*Hylobates*) fall into a single genus with several species and probably several sub-species also.

² In the *Proceedings of the Zoological Society*, 7th March 1899, will be found an admirable comparison, by Keith, of the general systematic anatomy of Chimpanzee and Gorilla.

as reminiscent of climbing habits: at least this is suggested by the distribution of "syndactylism" in the Mammalia. The hair is long with a woolly undergrowth¹. In young specimens it covers all parts save the face and certain portions of the hands and feet. Thus the palm and sole are entirely glabrous. Hairs are numerous on the back of the hand. On the thumb, they are found on the back of the metacarpal bone, but not beyond this. On the other digits, hairs are usually found on the back of the proximal phalanx, and in older specimens on the terminal phalanx, but not intermediately. In the foot, the hairs of the dorsal aspect are continued as far as the dorsum of the first or proximal phalanx of the great toe (hallux). On the remaining toes, the back of the proximal phalanx bears a few hairs, while the rest of the digit is quite glabrous in young individuals. Older examples may have hairs very scantily disposed on the terminal phalanx, but none on the second phalanx. The hairs are said to be implanted in groups of five on the head and torso, and herein the Gorilla is contrasted with the Chimpanzee.

The colour of the hair is of a "dusty" grey tint, for each hair is "banded," the root and tip being grey with an intervening zone of black. Thus again the Gorilla differs from the Chimpanzee (with its distinctly black hair relieved by local patches of white). At the same time, the "banded" hair of the Gorilla suggests that of the *Cynocephalous* monkeys, or of the *Mangabeys*; moreover the resemblance is confirmed by the presence (in many Gorillas) of a patch of reddish hair on the crown. The elongated face provides a further suggestion of similarity to the Baboons (*Cynocephali*).

The head is of great size, on account of the enormous jaws and the large masses of muscle developed in relation to these. The profile (Fig. 101) shews almost complete absence of any nasal projection, though the nostrils are bounded by a remarkably thickened elevation. This elevation, the "short" upper lip, and the small size of the ear, constitute points of distinction from the Chimpanzee, as may be seen from the illustration (Fig. 102). It is perhaps noteworthy, that the largest and most powerful ape should possess ears so reduced in size. (The Orang-utan when compared

¹ Forbes in Allen's *Naturalist's Handbook*, *Monkeys*, Vol. II.

with the smaller *Hylobates*, shews that the Asiatic *Simiidae* follow the same rule¹.)

The thorax is of great width and depth though relatively short; hence the trunk is stout and this appearance is enhanced by the protruding paunch of well-nourished individuals. The stomach is of enormous size in an adult male specimen (*Mus. Anat. Cant. Cy*), and capable of containing many pounds by weight of the vegetable food on which these animals chiefly subsist.

The external genitalia are remarkable for their small size even in adult male individuals. Ischial callosities are absent (as in all the *Simiidae* save *Hylobates*). Since the staple diet of the Gorilla is neither scarce nor difficult to obtain, an explanation of the



Fig. 101. Head of adult male Gorilla.
(Holt Don., *Mus. Anat. Cant.*)



Fig. 102. Head of adult female
Chimpanzee. (*Mus. Anat. Cant.*)

colossal strength of this anthropoid ape must be sought in another connexion. On the whole it seems probably indicative of the need for protection from enemies newly encountered when arboreal life is first or partly abandoned. These peculiarities of the Gorilla suggest therefore that we are dealing with a form which has been enabled to survive by the fulfilment of that condition. The general structure leads to the conclusion that the ancestors of the Gorilla were more definitely arboreal than their descendants. Certain contrivances seem to be indispensable by way of providing for the erect attitude, when the "raw material," so to speak, is "primate." The Gorilla has progressed further than any other of

¹ Cf. Pocock, *P.Z.S.*, 1905, Vol. II. p. 179.

the Simiidae towards the stage reached by Man himself. And this must be recognized on morphological grounds, even though we agree with Mr Pocock¹ in admitting that in fact the Chimpanzee actually moves (in bipedal fashion) more rapidly and freely than the Gorilla. Bulk and mass have to be considered here, and it is perhaps not flippanant to suggest that the smaller and weaker Chimpanzee like the *Hylobates* (which is the smallest anthropoid ape and yet the best "bipedal" performer of all) is by the greater development of these powers compensated for the brute strength which allows the Gorilla to move in more leisurely fashion.

B. **Hair.** The disposition of hair-tracts may be described briefly as follows (young specimens in the Cambridge Collection providing the materials for study).

(a) Sinus hairs. In young individuals, these are found definitely in four regions of the face and thus constitute the supra-orbital, infra-nasal, superior and inferior labial groups. I am unable to assure myself of their presence on the cheeks, though I suspect this. Nor can I see that the regions of implantation are distinguished either by elevations of the epidermis or by modified pigmentation (as in the Lemurs).

(b) From the brows the scalp hairs stream backwards cranio-caudally. At the temples the stream turns downwards, and sweeps past the ear in two subdivisions—the anterior of these passing in front of the ear and turning somewhat forwards at the angle of the jaw. The hinder stream is directed downwards on the neck.

(c) No vortex was observed in the nuchal region nor over the seventh cervical spine.

(d) Lateral vortices are not present on the abdominal wall.

(e) Anteriorly, such vortices are seen in two situations, viz. (i) over the clavicle as in *Tarsius* and in Man, (ii) in the inguinal region near the anterior superior spine of the ilium.

(f) Hair-tracts converge to the elbow, as in many of the Cercopithecidae, and in all the Simiidae save in certain examples of *Hylobates agilis*.

¹ P. Z. S., 1905, Vol. II. p. 178.

(g) A vortex is indicated at the wrist near the styloid process of the radius. There seems to be a tendency to the production of vortices near parts of the skeleton (such as this, the clavicle, and the anterior iliac spine) which lie immediately beneath the skin.



Fig. 103. Cutaneous grooves on the palm (vola) of a young Gorilla in the Cambridge Collection (1/1).

C. **Skin Colour.** The exposed parts of the skin are of uniform colour, viz. a dark slate-grey or black. Even the youngest specimens are as darkly pigmented as adult examples. The

Gorilla is thus very unlike the Chimpanzee, in which the skin is always lighter in tint, yellowish in the young and mottled with darker patches in adults. Of the Asiatic Simiidae, the *Hylobates*-

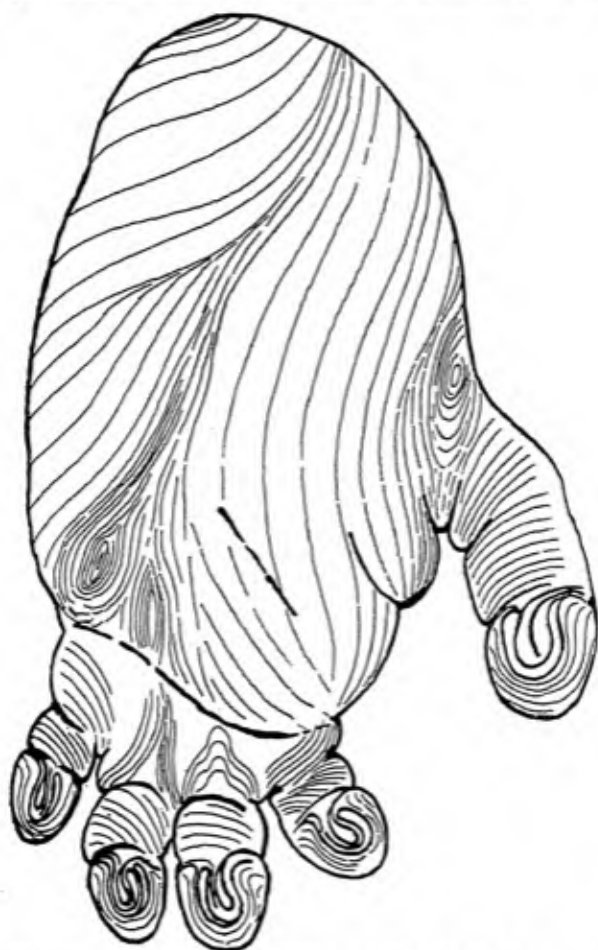


Fig. 103 A. Cutaneous grooves on the foot of a young Gorilla in the Cambridge Collection (1/1).

group shews an intense black pigmentation, while the Orang-utan is yellow-skinned.

D. **Hand and Foot.** In the hand and foot of the Gorilla as in the other Simiidae, the primitive pads are scarcely recognizable

as definite eminences save at the apices of the digits. This statement is more particularly applicable to the foot (Schlaginhaufen), where the great extension of surface provided by the heel is simply continuous with that of the proximal convexity in that region. The disposition of the papillary ridges now approaches that of Man in regard to its complexity if the hand be considered; while in certain plantar characters the human dispositions are the simpler of the two.

In the hand (Fig. 103), the thumb has a (relatively) small apical pad marked by a system of loops more complicated than in the remaining digits. Even so, the contrast with Man is greatest in respect of this part of the pollex and its cutaneous markings. The other finger tips are marked by a system of oblique loops or again vortices duplicati such as occur in *Macacus* (*v. supra*, p. 126). On the palm, certain tri-radial mark the position of three interdigital pads (not otherwise noticeable) corresponding to the second and following interdigital spaces.

On the plantar aspect of the foot (Fig. 103 A), the syndactylism of the digits other than the hallux is very striking. The figuræ tactiles are less striking than in the *Cercopithecidae* and a notable tendency is shewn (Fig. 104) to the development of two groups of parallel lines. Of the latter, one is on the fibular (outer) side of the sole and the lines are transversely directed. They receive great augmentation in the human foot, but in the Gorilla are less conspicuous than the longitudinal and oblique lines. These constitute the second group. They occupy the intermediate and tibial (or inner) areas of the plantar surface and suggest the mobility of the hallux. Two important features still demand

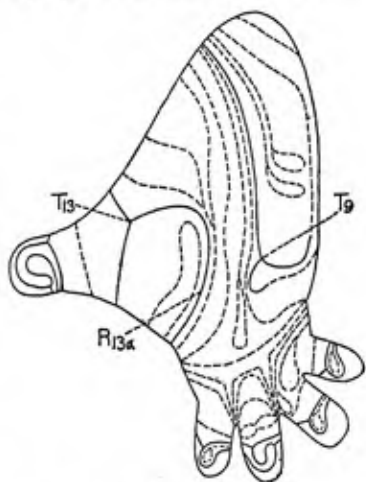


Fig. 104. Scheme of the cutaneous grooves on the sole of the foot of a Gorilla. Note the course taken by the line *R13a* and contrast this with Fig. 79. (From Schlaginhaufen.)

notice. The tri-radius T_{12} , already mentioned in connexion with the Cercopithecidae (cf. *supra*, p. 127), has now been thrust right on to the hallux: its divergent distal limbs no longer enclose a figura tactilis (Fig. 104), but merely a series of transverse lines. Its proximal limb (R_{12a}) is directed first transversely and then distally. Lastly the heel may now bear one or even two calcanean sinuses (Fersen-sinus of Schlaginhaufen), a character scarcely known in the lower Primates (though met with by Schlaginhaufen in *Macacus nemestrinus* with a frequency of 8.5 % for the single sinus only).

E. The Skeleton. (a) The skull. The first point to notice in an account of the skull of the Gorilla is the great difference that exists between male and female in the adult stages, and between the immature skull and the corresponding mature stage in either sex (cf. Figs. 105, 106). Museum specimens are most frequently skulls of adult or aged male individuals; female skulls of adults, and quite immature skulls of both sexes, come next in frequency, and the skulls that are the most profitable for the study of the typical features of the male, viz. specimens that have not quite reached maturity, and in which the permanent dentition is just about to be completed, are the most uncommon. Such a skull is described in detail below. Skulls of fully adult or aged male examples prove unsatisfactory for two reasons: in the first place, fusion of the various cranial bones is precocious, and hence the relations and connexions of the several bones are obscured at a comparatively early period; secondly, with maturity comes the immense development of bony ridges which indicate the great mass of the temporal and nuchal muscles. These ridges obscure the form of the brain-case. Equally impressive is the excavation of the bone by the extension of "air-sinuses." These pass principally into the region of the brow-ridges and the upper jaw (Fig. 107).

In the Gorilla, the apparatus of the jaws constitutes a factor dominating every part of the skull. The growth-changes have been mentioned already, and to some extent at least they are illustrated by the following illustrations (Figs. 105, 106). These are now supplemented by drawings (Figs. 108, 109) in which the

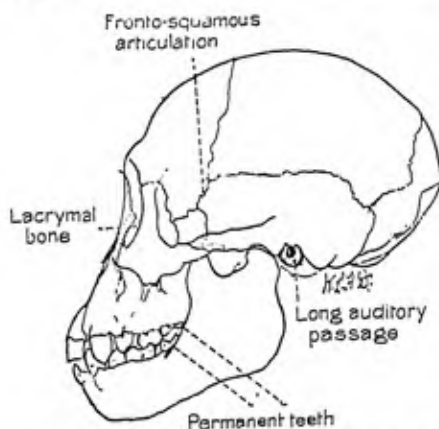


Fig. 105. Cranium, with mandible, of a young Gorilla (Simiidae); the first tooth of the permanent set has appeared (permanent molar tooth). Note the comparatively large brain-case. There is no auditory bulla: the auditory passage is long, but not so long as in adults: there are fronto-squamous and fronto-maxillary articulations. Osseous ridges and crests are still undeveloped ($\frac{1}{3}$ nat. size).

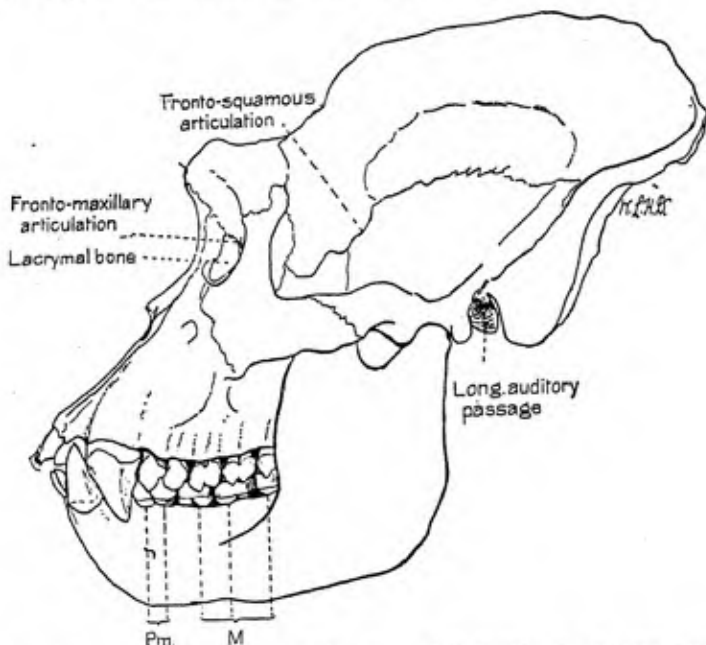


Fig. 106. Cranium, with mandible, of an adult Gorilla (Simiidae): note the absence of an auditory bulla, the presence of great bony crests, and of fronto-squamous and fronto-maxillary articulations (the latter within the orbit in place of a lachrymo-ethmoidal junction). The canine teeth are enormously developed in the male sex ($\frac{1}{3}$ nat. size).

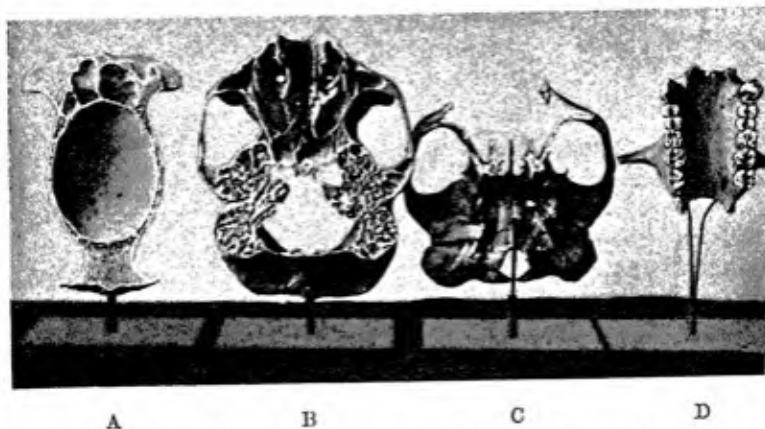


Fig. 107. Horizontal sections (of which the lower aspects are shewn) of the cranium of an adult male Gorilla.

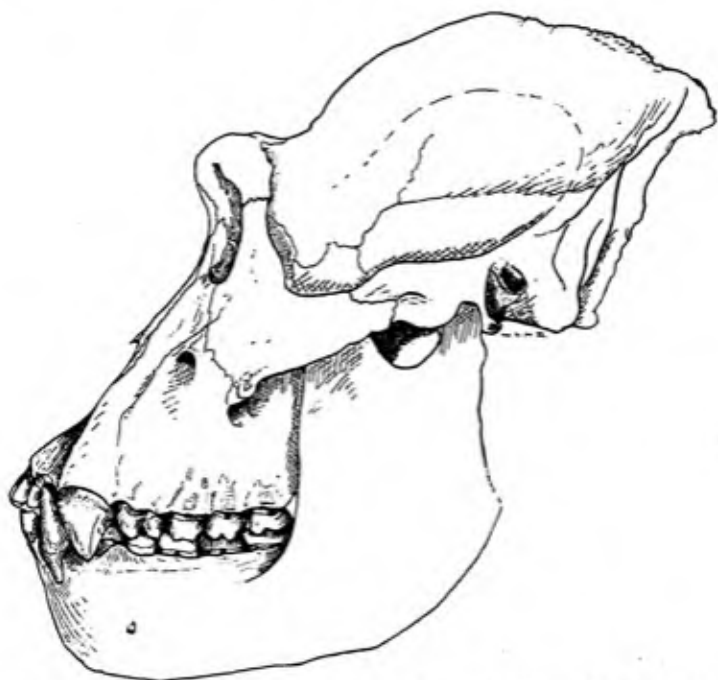


Fig. 108. Cranium of adult male Gorilla. (Liverpool Museum.) The mandible especially differs from that shewn in Fig. 106 ($\frac{1}{2}$ nat. size)

Gorilla is contrasted with the Chimpanzee. The details are reserved as more appropriate to the subject of the next chapter. Here we

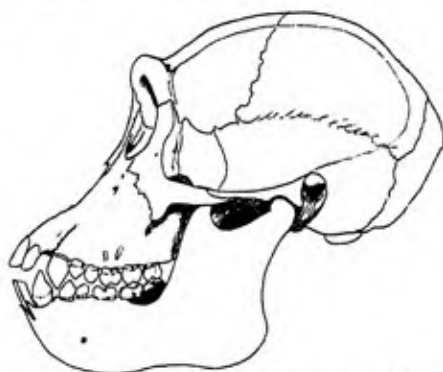


Fig. 109. Cranium of adult female Chimpanzee. (Mus. Anat. Cant.)
One-third of natural size.

may repeat that the outstanding effects are (a) extension of surface, so as to provide for an increased mass of muscle: this extension is effected largely by the outgrowth of osseous ridges (Fig. 110); (b) excavations of the osseous tissue, to reduce the otherwise inevitable increase in weight: these are brought about by the activity of cells in the mucous lining of the nose. Reference must be made also to the phenomena presented by the brain. For this study it is necessary to compare the appearances revealed by the skulls in section. This subject also is reserved for Chapter v. It will suffice to state here that nothing is more impressive in the Gorilla than the small amount of brain-growth after infancy, and this point will be discussed further in the place indicated (Fig. 158).



Fig. 110. Skull of an adult male Gorilla with an unusually high sagittal ridge or crest. (From a specimen in the Museum at Le Havre, Normandy.)

A systematic description of a skull of the Gorilla in the adolescent stage will now be given, and for this purpose the following divisions are convenient.

A. The true cranial part, consisting of the bones (developed mostly in membrane) which protect the cerebral hemispheres.

This part of the skull is ovate, longer and narrower (more dolichocephalic) in the Gorilla than in either Chimpanzee or Orang-utan, longer and narrower in the male than in the female Gorilla. Relatively to the facial part, it is small, the reverse of the human condition thus obtaining in the Gorilla. Yet the capacity is greater than in the other Simiidae. Thus Dr Oppenheim found fifteen out of twenty-two male crania with a capacity exceeding 500 c.c. The average value is given as 505 c.c. (for males) and the range as from 420 c.c. to 585 c.c. In the adult female Gorilla, the average value is but 475 c.c. though individuals may attain 555 c.c.¹ The coronal suture is less tortuous laterally than in its middle portion, where it meets the sagittal suture. The latter is quite tortuous until the period of closure begins, when the interlocking processes are reduced in length and the suture becomes simplified and straighter. The lambdoid suture is tortuous (till closure begins) as far as the temporal bone (the "Asterion"), thence downwards it is straight. The line of suture between the parietal and squamous bones is characteristically straight in its general direction, but the squamous bone overlaps the parietal with long tongue-like processes. The temporal margin of the parietal bone is very distinctly longer than the coronal margin, and constitute a notable difference from the human skull. Wormian bones are not uncommon in the sagittal and lambdoid sutures.

The muscular ridges have already been mentioned. In a young but nearly mature skull they converge rapidly from the external angular processes of the frontal bone, and each divides into upper and lower lines, the upper of which actually meet at the bregma though they diverge a little later. Herein a conspicuous difference from aged examples is offered by the adolescent Gorilla, for in the former the temporal ridges unite with one another to form a great sagittally-directed crest which occupies the line of the sagittal suture, and secondly, each temporal ridge combines with the corresponding portion of the superior nuchal line to form a similar crest which, running coronally and along the line of the lambdoid suture, is traceable at each extremity as a ridge which crosses the base of the stunted but massive mastoid process to join the zygoma, of which it forms the posterior root.

The zygomatic arches themselves are strongly developed though not much bowed outwardly, yet the channelling of the lateral cranial wall, especially along the line of the alisphenoid, leaves a very capacious temporal fossa. From the lambda, the contour-line of the skull descends sharply and obliquely forwards, towards the foramen magnum, the obliquity being very characteristic of the skull in all Simiidae.

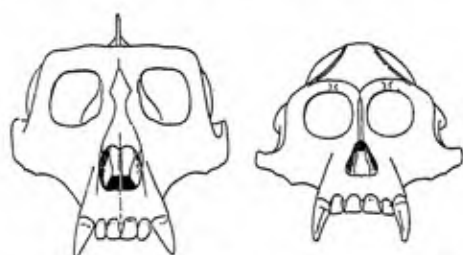
B. In the facial portion of the skull the orbits first claim attention. Bounded above by a great supra-orbital ridge which is continuous from one orbital margin to the other with scarcely any interruption, and which has been described as resembling a "pent-house," the orbits have a somewhat rectangular appearance, and though the angles are rounded off, yet the

¹ Cf. Oppenheim, *Z. für M. und A.*, Band xiv. 1911.

general aspect is quite distinct from the oval contour which characterizes the orbit in *Simia*. In this respect the Chimpanzee agrees with the Gorilla. The external angular processes of the frontal bone are massive and project strongly, and this also contributes to the square-cut appearance of this part of the face (Fig. 111).

The outer margins of the orbits are indistinct and bevelled.

The lachrymal bone is reduced as in Man and though abnormal cases of a well-developed lachrymal hamulus occur, yet in general this process is even more vestigial than in the human skull. The lachrymo-ethmoidal suture is usually replaced (65.4% as against 34.6% of lachrymo-ethmoidal sutures in a series of 26 males) by a fronto-maxillary suture which may indeed be of considerable length (10 mm.): the os planum of the ethmoid is reduced considerably in vertical extent and is particularly attenuated anteriorly. The number of infra-orbital foramina is variable, but the cases in which a single foramen occurs are just in excess of the other varieties.



Figs. 111, 112. Crania of Gorilla and *Simia*; the former is distinguished by the massive brow-ridges which are continuous from one orbit to the other.

The nasal bones (Figs. 113, 114, 115) are very characteristic in form, and are conjoined at an early epoch. The combined bones form a single element of the following shape. From a pointed apex on the level of the supra-orbital ridge, the margins diverge for about 10 mm. (at the level of the junction of the upper and middle thirds of the orbit); below this they approach one another again, and here a sharp crest projects from the middle line. Then the margins diverge strongly and the crest is lost at the same time. Finally the lateral margins for the last time converge, but only slightly. The nasal bones thus extend well below the level of the orbits, and their shape distinguishes the bones in the Gorilla equally from those of the Chimpanzee¹ and the Orang-utan. (Cf. Fig. 113 A, B, C.)

The lateral margins of the apertura pyriformis nasi are seen to be formed by the premaxillae which extend up even along the sides of the nasal bone.

¹ A male Chimpanzee skull in the Cambridge Collection presents a remarkable instance of the anomalous occurrence of nasal bones of the type here described as distinctive of the Gorilla.

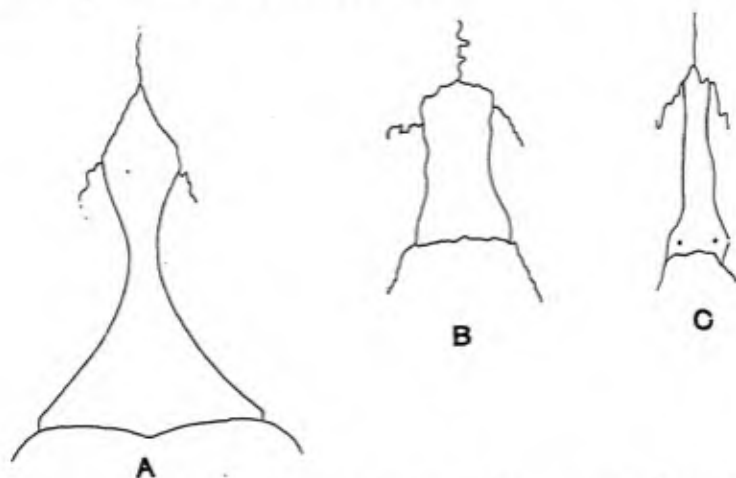


Fig. 113. Nasal bones of Simiidae; (A) Gorilla, (B) Chimpanzee, (C) Orang-utan.

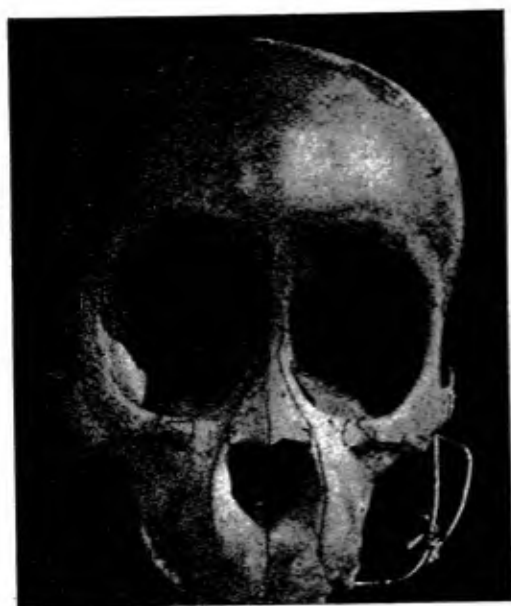


Fig. 114.



Fig. 115.

Fig. 114. Nasal bones and intermaxillary (premaxillary) bone of a young Gorilla.

Fig. 115. Diagram of the nasal bones and premaxilla in the preceding figure.

They are rounded, and the lower margins of the nasal apertures are quite indistinct. No definite nasal spine is seen, but sometimes a small tubercle occurs and in a good many cases the premaxilla throws off paired backwardly-directed processes to meet the nasal septum: these processes must not be mistaken for a true nasal spine, though suggestive of that structure. The alveoli of the great canine teeth form projections on the facial surface on each side of the nasal aperture.

The palate has the characteristic long hypsiloid anthropoid contour, and the post-palatine spine is commonly replaced by a notch. There is usually some irregularity in the arrangement of the sutures on the palatine surface, whereby the common cruciform appearance is distorted. The tuber maxillare is small, and the anterior palatine foramen (whence the premaxillo-maxillary sutures spring) is characterized by not including the lateral foramina (for the anterior palatine arteries).

The temporal fossa is very deep and capacious: the alisphenoid deeply channelled, and often attenuated above, in correlation with the common arrangement of a fronto-squamous articulation replacing the parieto-sphenoid junction (of the Orang-utan, of Man, and of the Cebidae and Lemuroidea): herein some of the lower human races and the Cercopithecidae agree with the Gorilla.

The infra-temporal crest is very small, and the speno-maxillary fissure much narrowed as in the other Simiidae, which in this respect (and the concomitant approximate completion of the post-orbital wall) are more highly specialized than Man or the Lemuroidea. Sometimes the malar bone does not provide the end-boundary of the speno-maxillary fissure, and then a speno-maxillary suture occurs.

The base of the skull offers a few points worthy of special note. Anomalous processes, such as the third occipital condyle, or ossification in the suspensory ligament of the axis, and the like, are rare. The condyles are short and the foramen smaller than in Man, even in skulls absolutely larger than the human skull. The glenoid fossa is very shallow and to its inner side is a great endo-glenoid tubercle. The anterior lacerate foramen is commonly closed by osseous deposit, and the styloid process is diminutive. The tympanic bone is long and semi-cylindrical, and has no "bullous" inflation (Fig. 116 B).

The teeth are of the typical number ($\frac{2133}{2133}$). The canines are enormous in the males: the premolars have commonly three roots in the upper jaw; the molars bear four very clean-cut ("crystalline" Dr Keith calls them) cusps in the maxilla; and in the mandible, a "talon" may bear two additional cusps, despite the statements in certain works on this subject. The third molar is already shewing signs of reduction in the maxilla (and the Chimpanzee shews a further advance on this condition of reduction). Accessory teeth are not uncommon. First in frequency come accessory molars in the maxilla, then remnants or rudiments behind the premolars in the maxilla. A unique case in the Hamburg museum shews a double canine tooth, and

sometimes a fifth incisor (of large size and so probably not a retained milk tooth) is seen in the mandible. Further details as to the dentition are provided and commented upon in Chapter VI.

The mandible is of enormous size and weight. The rami diverge but slightly and the post-canine teeth are set in two nearly parallel series. No prominence is seen in the symphyseal region, the chin being absent or retreating. The genial tubercles are not distinct, for they are usually represented by a vertical ridge much nearer the lower border of the symphysis

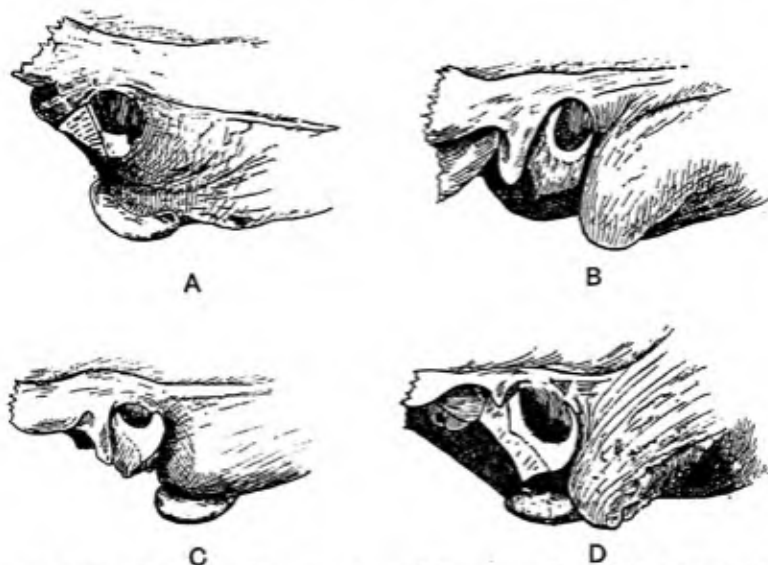


Fig. 116. The left auditory meatus and its surroundings in A, Orang-utan; B, Gorilla; C, Chimpanzee; and D, Man (Swat river tribesman). The parts to be noticed specially are: i. the tympanic bone which is below the meatus, and has a different form in each case; ii. the conoid process, which is in front of the meatus, and much smaller in Man than in the Apes; iii. the mastoid process, which is behind the meatus, and in the Gorilla is not unlike that of Man. (W. L. H. D. del. from specimens in the Cambridge Collection.)

than the corresponding tubercles in Man. The anterior belly of the M. digastricus makes little or no impression on the bone, the mylo-hyoid ridge is absent, and the mylo-hyoid groove, though recognizable, is shallow save where it commences beneath the flange-like lingula. The ascending ramus is very high, and the sigmoid notch shallow, but the coronoid process extends above the level of the condyle. Altogether this region of the mandible offers a special contrast with the human jaw. The condylar neck is short and the condyle flattened. This character bears some relation to the form of the glenoid fossa, which is, as above described, shallow. The shallowness might be held to indicate free lateral movements of the mandible in mastication.

Such a conclusion would be erroneous, for the fact that the canine teeth surpass those adjacent to them in height, favours a simple hinge-like movement of the temporo-mandibular joint. This is an important distinction from the human arrangement (and the accuracy of the conclusion is confirmed by the small size of the external pterygoid plates). Such movements of the mandible react on the mode of abrasion of the dental crowns¹, a matter to be discussed in the sequel.

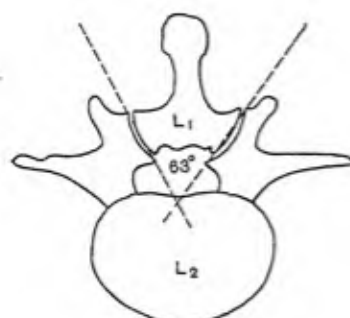
These notes refer more particularly to the skull of a young male individual. The adult male differs in certain features which have been indicated above. In female skulls, the permanent characters resemble those set forth in detail here, since the intensive development of the distinctive male features never occurs. On the other hand, very immature examples also present distinctive characters, and on the whole they may be considered to approximate more nearly to the human cranial type. In fact the gorilla-type diverges from that of Man at an early period, the contrast becoming more marked with the increase in age.

(b) **The Vertebral Column.** In the cervical region of the vertebral column the enormous length of the vertebral spines is the most striking feature: these spinous processes are not however bifid, and thus differ from those of the existing human races of Europe although approached in this respect by the cervical vertebrae of some of the primitive human races in other regions, and also the prehistoric skeleton from La Chapelle aux Saints in France. The costal process is sometimes imperfect, so that there is no canal between it and the true transverse process. The costal process of the sixth cervical vertebra is large, while that of the seventh is very small, the same proportions obtaining as in Man.

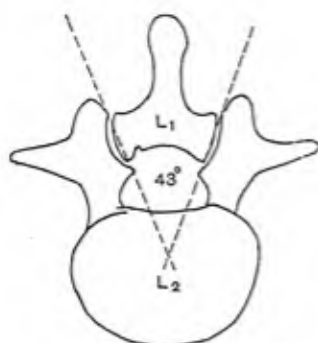
In the thoracic region thirteen vertebrae are common, though occasionally fourteen rib-bearing vertebrae occur. Their centra appear as though laterally compressed (in comparison with those of Man): the transverse processes are stunted but massive: the spinous processes of the lower members of this series tend to be bifurcated. The section of the thorax in the horizontal plane differs from that of Man in the relatively larger proportion borne by the antero-posterior to the transverse diameter. The thorax is thus intermediate between the human type, and the pithecoïd form as shewn by Cercopithecidae.

The usual number of lumbar vertebrae is three (Fig. 118), although four vertebrae are of frequent occurrence.

¹ Cf. Keith, *Proc. Roy. Soc. Medicine, Odont. Section*, 1913, p. 16 of reprint.



(A)



(B)

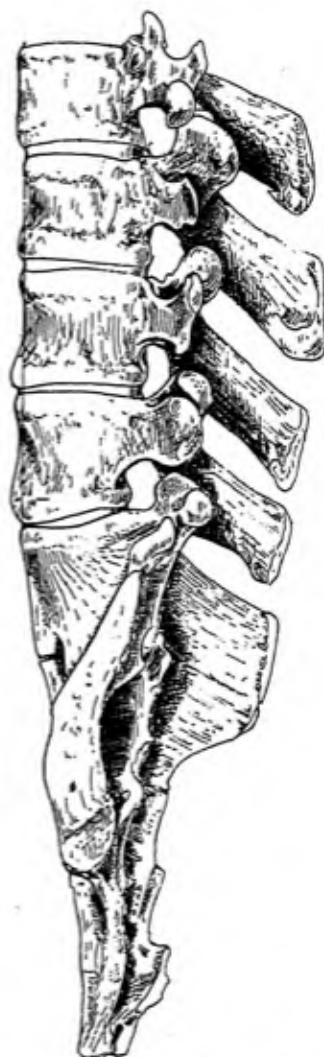


Fig. 118.

Fig. 117.

Fig. 117. Diagrams of the articulations between two lumbar vertebrae, (A) of Gorilla, (B) of Man, to shew the more complete interlocking in the latter example.

Fig. 118. The last thoracic and the lumbar vertebrae of a Gorilla, together with the sacrum. The slight anterior concavity of this part of the vertebral column is to be noted. Cf. also Fig. 81 for anapophyses. (W. L. H. D. del.)

The lumbar centra are vertically higher and transversely narrower than those of Man. While the lateral and mammillary processes are well developed, the accessory is insignificant. Anapophyses are not seen, but sometimes they occur in the Orang-utan.

The "transverse" process of the third lumbar vertebra is small in comparison with the others and thus differs from its representative in Man. The interlocking of the vertebrae, brought about by the superior articular processes of one vertebra embracing the lower processes of the vertebra above, is much less effective and complete than in Man; for the former processes do not extend so far round the latter as in Man and their hold is correspondingly more feeble. The two forms are represented in Fig. 117. The differences between the vertebral columns of Man and Gorilla are extraordinarily well marked in this region, which is profoundly modified in correspondence with the difference between the erect attitude of Man and the crouching one of the anthropoid ape.

The sacrum (Fig. 118) of the Gorilla consists usually of six pieces; the laminae of these unite posteriorly with remarkable constancy and regularity: the variety of spina bifida which consists of a lack of union of these laminae is thus of infrequent occurrence. A well-marked sacral notch is usual, and is due to the comparative attenuation of the second sacral vertebra¹. The coccyx is rudimentary as in Man. The sacral index is stated by Turner to be 72 (Homo 112): and the curvature is small, the average depth of the sacral curve being 10.4 mm. (Paterson) as against 25.1 mm. in the (white) Hominidae.

A general review of the characters of the vertebral column shews that the Gorilla differs from Man in respect of the degree of anterior lumbar curvature (Fig. 118). As regards the vertebral foramina, these are throughout more circular in outline than in Man; nor as regards the centra of the vertebrae does the Gorilla shew in the cervical and lumbar² regions the marked excess of the transverse over the sagittal diameter so characteristic of the corresponding human vertebrae. In fact, the vertebral column of the Gorilla

¹ Cf. Paterson, *The Human Sacrum*, p. 132.

² The specimen shewn in Fig. 117 (A) does not conform to this statement.

would be inadequate to the task of supporting the weight of the head and of the upper limbs, were not the latter still employed as supports and thus as a means of relieving the strain borne entirely by the vertebral column in the human type.

The pelvis is much more elongated in the cranio-caudal direction than is the case in the human skeleton. The iliac crests are more sinuous, and the iliac fossae more hollow than in any other anthropoid ape, though less so than in Man, and an anterior inferior iliac spine is sometimes found (cf. Chapter XII). The posterior parts of the ilia are less developed and the ischial tuberosities are less massive than in Man. The Os innominatum is long, and deficient in iliac breadth when compared with the corresponding human bone. The pelvic brim is, relatively to its sagittal diameter, much narrower than that of Man. Yet in general, the pelvis offers a good demonstration of the modifications necessary for the conversion of this skeletal element from the pronograde type of the lower Primates to the orthograde human type. But the changes are approaching completion in the Gorilla, for this animal presents a pelvis of aspect more nearly human than any other ape can provide. Similar conclusions are to be drawn from the bones of the limb-girdles, limbs and thorax. A few supplementary details will now be added.

The femur is short, stout, and straight; the shaft entirely lacks the *linea aspera* which is so characteristic of the human femur, being flattened sagittally. The neck is short, and the articular surface of the head less extensive than in Man. It makes an angle of about 124° with the shaft. In Man this angle varies from 128° — 141° . As in Man (but unlike the condition in the Orang-utan), the ligamentum teres is found. In the knee-joint the external cartilage is annular, not semi-lunar (cf. Fig. 119). On the tibia no soleal line is seen, and the plane of articulation with the astragalus is very oblique. The fibula is very slender and its malleolus small. The calcaneum is longer and larger than in the other Simiidae, but even thus it falls far behind that of Man in these respects. The first metatarso-tarsal articulation is clearly a ginglymus joint, and contrasts strongly with that of Man, the difference being evidently referable to functional adaptation.

The scapula contrasts strongly with that of Man in respect of the large extent of the supra-spinous fossa. The scapula otherwise resembles the human scapula more closely than do those of the Chimpanzee and the Orang-utan. Paradoxically, the clavicle is comparatively weak and slender, lacking as it does the massive character of its representative in the Orang-utan. The humerus is characterized by a similar lack of definition as regards the evidence it bears of the attachment of muscles and ligaments: thus the deltoid muscle makes but little impression on the shaft,

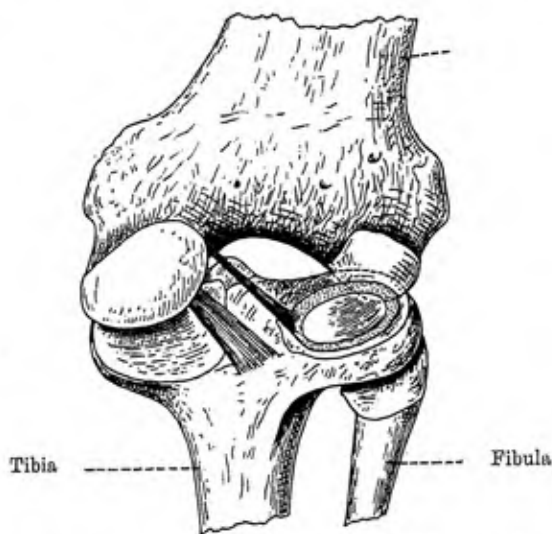


Fig. 119. Posterior aspect of the knee-joint of a young Gorilla (right limb), shewing the annular form of the external articular cartilage.

which indicates the relatively small size and functional activity of this muscle in the Gorilla. The average figure representative of the angle of torsion of the humeral shaft is given by Broca as 141° , European Hominidae providing an average of 161° .

The olecranon fossa of the ulna is very frequently perforated (in about 80% of examples). The shafts of the radius and ulna are not so straight as in the corresponding human bones, and consequently the intermediate space is more extensive. In the carpus, the ossa centrale and radiale fuse as in Man (unlike their

condition in the Orang, Hylobates and in the Cercopithecidae) to form the scaphoid bone of the wrist.

The sternum is flat (platisternal) and the junction of pre- and meso-sternum occurs at the level of the third costal cartilage more commonly than in Man, but less usually than in Hylobates.

The following numerical data are taken from Aeby's work on the Osteology of the Gorilla¹.

Proportions of the several segments of the limbs:

Upper limb: Arm 41.1%. Forearm 32.7%. Hand 26.2%.

Lower limb: Thigh 41.3%. Leg 30.5%. Foot 28.2%.

F. Muscular System². The muscular system now claims attention and will be considered in the same way as in the accounts of the Lemuroidea, the Tarsii and the Cercopithecidae.

The muscles correspond severally with very close accuracy to those of Man, and in fact the number of distinctive human muscles, at one time thought to be thirteen, is now reduced to three (*M. plantaris*, *peroneus tertius* and *serratus posticus inferior*). The acromio-trachelian and dorsi-epitrochlear muscles distinguish the Gorilla, not being normal in Man.

While a general agreement in the individual muscles exists, there is a definite distinction to be drawn as regards their relative development in Man and in the Anthropoid Apes. Thus while Man is characterized by the development of the musculature of the lower limb, in the Gorilla that of the upper limb has been developed. The musculature of the upper limb bears to that of the lower limb the proportion of $\frac{1}{1.02}$ by weight in the Orang-utan (the proportion in the Gorilla will be about the same), while the proportion in Man is $\frac{1}{3}$. At the same time, when the upper limbs of the Gorilla and Man are compared, it will be seen that in the Gorilla the extensor series of muscles falls far behind that of Man in relative development (16% instead of 22% of the total musculature³).

¹ *Morphologisches Jahrbuch*, Band iv.

² See the bibliography published by Keith in *Natural Science*, 1897. Also Kohlbrugge, 1896 *op. cit.* More recently, Sommer has published an important paper in the *Jenaische Zeitschrift*, Band XLII. S. 181.

³ Langer, *Sitz. der k. k. Akad. der Wiss. Wien*, Band LXXIX. Abth. 3. SS. 177 *et seq.*

The remainder of this account will be subdivided into sections in the same way as in the other animals described.

1. Of the cutaneous muscles, *M. platysma* is notable for its extraordinary coarseness (cf. Fig. 120). Differentiation of the muscles of expression has reached a stage not far removed from that obtaining in Man. The dorso-humeral muscle has disappeared, save in anomalous instances where it appears as an "Achsel-bogen" or axillary band.



Fig. 120. Facial musculature of an adult Gorilla. Note the great development of the anterior fibres of the platysma. The specimen forms part of the Holt donation to the Cambridge Collection. (Specimen Cy.)

2. In an adult male Gorilla, I found the *M. digastricus* to consist of the normal anterior and posterior parts. The tendon is long and stout so that it is clearly traceable through the *M. sterno-hyoideus*. The anterior belly is a wide sheet arising partly from the hyoid bone. It quickly approaches its fellow of the opposite side, the triangular gap between the two being largely composed of fibrous tissue. Near the symphysis, the deeper fibres are attached to the margin of the mandible, the attachment being simply linear, but continuous from side to side of the middle line. The more superficial fibres spread out into a connective tissue

sheet, which is lost on the facial aspect of the symphysial region. The tendinous "arcade" from which the anterior muscle arises in the Cercopithecidae, is thus vestigial only. No decussation of the anterior bellies was noticed, though I found this condition in an adult male Orang-utan. On the whole, the anterior belly of the *M. digastricus* is to be contrasted strongly with that of Man, in whom it has become so massive that some notable accession of function must have occurred. I would suggest that of the various possible factors, two are worthy of particular notice. Thus we should remark that the muscle varies in size inversely with the mass of the mandible. And again, the increase in the muscle is accompanied by an increase in the angle at which the two halves of the mandible are inclined to one another. Consequently we may suppose that with a lighter mandible, the employment of a more powerful depressor of the chin is advantageous: in Man the *M. digastricus* has met this demand. Again, the widened space within the jaw necessitates a more powerful sublingual support for the tongue. And the human *M. digastricus* serves this purpose also.

3. The sternal and clavicular parts of the *M. sterno-mastoid* resemble those of the Cercopithecids in their distinctness. But the clavicular part is weaker than the sternal component, so that a contrast here exists between the Gorilla and the lower monkeys. As regards the cranial attachment of the muscles, a marked extension over the occipital bone is noteworthy. This is provided by the sternal component of the conjoint muscle, and the mechanical advantage of such an extension is quite clearly appropriate to the enormous skull.

4. The *M. trapezius* has also a wide area of cranial attachment, but on the other hand it extends down the spine to the tenth thoracic vertebra only, and does not overlap the *M. latissimus dorsi*. It appears therefore that the lower part of this muscle is defective in comparison with that of Man, while the upper part is more extensive. This suggests that the latter (the cranial portion) is influenced by the great weight of the cranium, while the lower part has assumed in Man new functions related to the erect attitude. The general characters of the *Mm. rhomboideus*, *omohyoides*, *levator anguli scapulae*, and *deltoideus* are

reminiscent of those found in the *Cercopithec*i, though departures in the direction of the characteristic human disposition of these muscles are numerous. On the whole, however, distinct evidence of affinity with the lower forms persists. And this indicates that the predominant use of the fore-limb in climbing has been effective in securing the retention of the appropriate arrangement.

The osseous origin of the *M. latissimus dorsi* is of particular interest, in view of the relation of this muscle to movements involved by an arboreal mode of existence; the muscle arises from the tenth and succeeding vertebral spines, and in its attachment to the crista ilii is found to be much more extensive than in Man, for it arises along the whole length of this bony crest (in the Chimpanzee it may even encroach upon the region of Poupart's ligament). The tendon of insertion has relations with that of *M. teres major* similar to those described in the *Cercopithecidae* (*v. supra*).

The *M. dorsi-epitrochlearis* needs no special description, but its retention would appear to be determined by that of the use of the limb for climbing. The chief characteristic of the *M. teres major* is the occasional great breadth of its scapular attachment.

The *M. pectoralis major* closely resembles that of Man. The lowest fibres usually constitute an independent muscle, the "*pars abdominalis*."¹ The insertion of the *M. pectoralis major* is sometimes carried to the tendon of the *M. coraco-brachialis*. The *M. pectoralis minor* (Fig. 121) also resembles its counterpart in Man, though its costal attachment is more extensive (as far as the seventh rib in some cases) and it is subdivided by the great laryngeal sac which perforates it and protrudes in the axilla. On the whole however the muscles of the pectoral region approach more nearly the human condition than do those of the nuchal and dorsal regions.

5. The *M. coraco-brachialis* is frequently double², and consists then of a long and a short portion. The muscle may be found conjoined with (a) *M. latissimus dorsi*, (b) *M. triceps* or (c) *M.*

¹ Windle, "The Pectoral Group of Muscles," *Trans. Roy. Irish Acad.* Vol. xxix. part xii. This muscle, arising from the aponeurosis of the *M. obliquus externus*, is sometimes termed *M. pectoralis quartus*. In Man, it blends with the costal portion of the *M. pectoralis major*.

² It is however single in the adult Gorilla (Cy) dissected by the writer at Cambridge.

brachialis anticus. It has been recently suggested¹ that in respect of the *M. biceps humeri* the Simiidae are more highly specialized than the Hominidae; the evidence rests on the reduction observed in the *lacertus fibrosus*, or fascial expansion of the tendon of insertion; the Simiidae seem to have passed through a stage of evolution in which the muscle in question possessed three heads of origin.



Fig. 121. A dissection of the pectoral and axillary regions in an adult Gorilla (Specimen Cy); the references are as follows:

1. *M. pectoralis abdominalis* (chondro-epitrochlearis). 2. *M. pectoralis major* (out). 3. *M. pectoralis minor*. 4. Laryngeal sac extending into the axilla. 5. Tendon of *M. latissimus dorsi*, with the *M. latissimo-condyleus* extending down the arm.

6. The tendon of the *M. flexor longus pollicis* is sometimes absent, sometimes represented by a mere thread arising from the tendon of the deep flexor of the index, or from the anterior carpal ligament.

The *M. extensor minimi digiti* is represented by a tendon from the *M. extensor communis digitorum*.

The *M. extensor indicis* resembles its counterpart in Man. As for the extensors of the pollex, it is noteworthy that a *M. extensor*

¹ Grönroos, *Abh. der Akad. der Wiss. zu Berlin*, 1903.

pollicis brevis, though by no means constant, is nevertheless sometimes met with. This is another instance of a transitional phase in the evolution of a series of muscles and tendons. Conversely, in Man, the *M. extensor pollicis brevis* may be greatly reduced. In a human subject dissected at Cambridge (21. xi. 1910) the remnant appeared as a mere appendage of the *M. extensor pollicis longus*.

7. The diaphragm is characterized by the large proportions of the tendinous part, which leaves but a narrow zone of muscular fibre around its periphery. The pillars of the diaphragm are arranged as in Man.

It is reasonable to suppose that this muscle has become as predominant a factor in respiration as in Man. Thus for instance accessory muscles of respiration, such as the scaleni, possess no greater extent¹ than in the human body. In the pronograde *Cercopithecidae*, on the other hand, they are attached to ribs more caudally placed.

8. The muscles of the hip and lower limb provide many suggestions of the gradual approach to human conditions. A survey of the muscles about to be described will shew that the essential differences may be related to

(a) The size of a muscle: ex. gr. *M. gluteus maximus*.

(b) The extension of attachment in different types: ex. gr. *M. gluteus maximus* and *M. soleus*.

(c) The position of the muscles in regard to joints, and also their inclination to the axis of the limb: ex. gr. *M. adductor longus* (primus), which in Man migrates towards the body of the pubic bone.

(d) The coalescence of muscles once separated: ex. gr. the components of the *M. biceps femoris* and *M. adductor magnus* (of Man).

Some of the evidence on these points will now be given.

The *M. gluteus maximus* arises from a fascia covering the *M. gluteus medius*, from the posterior part of the iliac crest, from the sacrum, greater sacro-sciatic ligament, and tuber ischii; the

¹ Kohlbrugge, *op. cit.*, p. 43; cf. also the suggestive paper by Wood-Jones in the *J. A. P.*, Vol. XLVII. 1913.

sacral portion is the largest, and the ischial part has been described as a separate muscle, the *M. ischio-femoralis* (Duvernoy). The *M. scansorius* is said to be merged in the *M. gluteus minimus*.

The *M. biceps femoris* commonly consists of two distinct portions, as in Chimpanzees (cf. Fig. 122).

The adductors of the thigh comprise four muscles arranged in the following manner (Deniker).

The *M. adductor primus* corresponds to the *M. adductor longus* of human anatomy, and is attached to the horizontal ramus of the *Os pubis* and not to the body of that bone, as in Man. The *M. adductor secundus* corresponds to the *M. adductor brevis* of Man, and is attached to the body of the *Os pubis*. The *M. adductor tertius* (corresponding to the upper part of the *M. adductor magnus*) of Man is attached to the descending ramus of the pubis and also to the *linea aspera* of the femur. It sends a slip to the *M. adductor secundus*.

Lastly, there is the *M. ischio-condyleus*, which corresponds to the condylar portion of the *M. adductor magnus* of Man. The separate existence of this ischio-condylar muscle is very characteristic of *Cercopithecidae* and *Simiidae*. It encroaches at its insertion upon the popliteal area of the femur.

The *M. gracilis* is very wide throughout, and at its insertion it extends into the deep fascia of the leg and thus to the lower part of the tibia.

Of the *M. quadriceps extensor cruris*, the component *M. rectus* may present a bicipital conformation, as in Man.

The *M. psoas minor* is variable in its occurrence, being rather more frequently absent (60%) than present (40%) (Keith).

The *M. soleus* is of interest, inasmuch as it has been found in the Gorilla with an occasional tibial origin. Otherwise it follows the rule for *Cercopithecidae*, and has only a fibular origin.

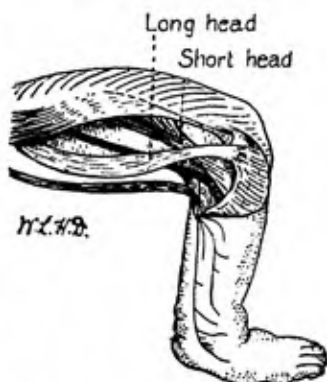


Fig. 122. Dissection of the outer side of the thigh of an adult female Chimpanzee, shewing the two heads of the *M. biceps*: also the great sciatic nerve and its division.

The *M. plantaris* never appears to be developed in the Gorilla as a separate muscle, although it is of common occurrence in the Chimpanzee. The fascia plantaris is described by Sommer¹ as being very strong. Loth² dissected the fascia in a Chimpanzee and an Orang-utan and found the tibial component well developed, though the fibular part was weak in comparison with the condition presented by it in *Cynocephali*.

The *M. flexor accessorius digitorum* (*M. quadratus plantae*) is rare, though it has been found in Gorilla (its mode of insertion in the Simiidae is also unlike that of Man, as it may in Chimpanzees form an attachment to the tendons of the *M. flexor brevis digitorum*).

The tendons of the plantar aspect of the foot are arranged as follows.

M. flexor brevis digitorum. This muscle shews a distinct approach to the human condition, inasmuch as its superficial head takes origin partly from the os calcis, and not only from the fascia plantaris as in the lower Primates generally. This superficial part provides (perforated) tendons for digits II and III (more rarely II, III and IV).

The deep head of the muscle arises from the tendon of the *M. flexor longus digitorum*, and provides perforated tendons for digits IV and V, though the last-mentioned is often absent³. As regards the long flexor muscles of the hallux and digits, Hepburn⁴ found the Gorilla to be the anthropoid ape most nearly resembling Man. The *M. flexor longus hallucis* contributes a strong slip of tendon to that of the *M. flexor longus digitorum*. In regard to all these plantar structures, the Orang-utan retains its distinction as an aberrant form.

The pedal interosseous muscles are grouped about the third digit, and herein the Gorilla differs from Man and resembles the Chimpanzee, the Orang-utan, some varieties of Gibbon, and the Cercopithecidae generally: it must be admitted that many Gorillas possess the human arrangement, these muscles being then grouped about an axis formed by the second digit. In this respect the

¹ *Jenaische Zeitschrift*, 1906.

² *op. cit.* p. 135 *supra*.

³ Sawalischin, *Morphologisches Jahrbuch*, Band XLII. Heft 4, with literature.

⁴ *Cf. J. A. P.*, 1892.

Gorilla is in a phase of evolution which is transitional and intermediate between Hominidae and the other Simiidae¹.

G. Vascular System. The heart closely resembles the human organ: in respect of length it bears to the stature a ratio slightly higher than is the case in Man. In position it is turned as much to the left side of the thorax as is the human heart², and thus the Gorilla stands in strong contrast with the Cercopithecidae.

The arrangement of the great arteries springing from the arch of the aorta is identical with that of Man in 89% of examples. The foregoing characters bear some relation to the increased width of the thorax found in the erect and semi-erect Primates. A few notes on the peripheral vessels will now be added.

The axillary artery resembles that of Man in its upper portion³, but in the lower part, the presence of a common trunk of origin for the circumflex arteries of the scapula and humerus (anterior and posterior circumflex arteries and the "dorsalis scapulae"), constitutes a distinct retention of the conditions met with in the Cercopithecidae.

The A. brachialis lies superficially to the median nerve. It is thus an A. brachialis superficialis (not commonly retained in Man) and it gives off the radial and ulnar arteries. The ulnar artery asserts itself more distinctly than in the Cercopithecidae as a channel of supply to the palmar aspect of the hand. Its superficial division supplies the little finger and the ulnar aspect of the ring finger, the superficial palmar arch being as yet undeveloped. The deep division joins the radial artery to form a distinct "deep" arch, to which the radial contribution is the greater.

The striking feature of the arteries in the lower limb is the retention of the A. saphena. This vessel may be regarded as an archaic possession, occurring occasionally in Man as an anomaly. The plantar arteries resemble those in the human foot, save that they are relatively smaller, the *dorsal* contribution to the deep

¹ The Mm. contrahentes are rare in Gorilla (Keith, *Proc. Zool. Soc.* 1899, March 7).

² Eisler, *Das Gefäß- und periphere Nervensystem des Gorilla*; Ruge, *Morphologisches Jahrbuch*, Band XIX, with illustrations.

³ Manners Smith, *J. A. P.*, Vols. XLIV, XLV, XLVI. I have checked the descriptions by reference to dissections in the Cambridge Museum.

plantar arterial arch being still predominant. Such dispositions of the limb arteries are determined by the pressure to which various aspects of the respective limbs are subject. This pressure will in turn be influenced by the functions of the limb. Thus the lack of full development of the superficial palmar arteries suggests that the hand has not been emancipated fully from its use as a support in locomotion. Again, the use and form of the lower limb permit of the retention of the A. saphena, and this results in a greater supply to the plantar aspect of the foot *via* the A. dorsalis pedis (the continuation of the A. saphena).

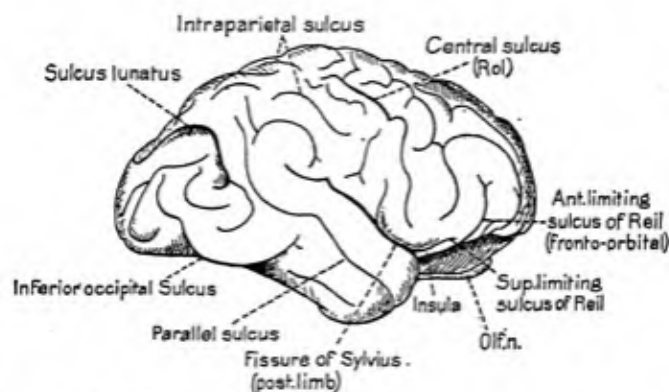


Fig. 123. Lateral aspect of the right cerebral hemisphere of a young Gorilla (Simiidae). The olfactory nerves are attenuated in point of size: the cerebral surface is much more convoluted than in the preceding examples and recalls the appearance of the human cerebrum. (Mus. Anat. Cant. Specimen Cr.)

H. Nervous System. The brain of the Gorilla (Figs. 123, 124) is much smaller than that of Man, but in regard to its conformation, it may be described as providing a sketch-plan of the human organ. The Simiidae have made a most distinct advance beyond the Cercopithecidae in respect of their cerebral characters, though the brain of *Hylobates* suggests the path pursued in evolution by the three larger forms (Orang-utan, Chimpanzee, and Gorilla). A brief account of the purely morphological conformation of the Gorilla's brain has been appended for purposes of reference, but here a few suggestions may be offered in regard to the nature of the Gorilla as revealed in the structure of its brain.

As remarked above, that organ presents no small degree of similarity to the human brain [the resemblance is rather more marked in the mesial aspect of the cerebrum than on its lateral

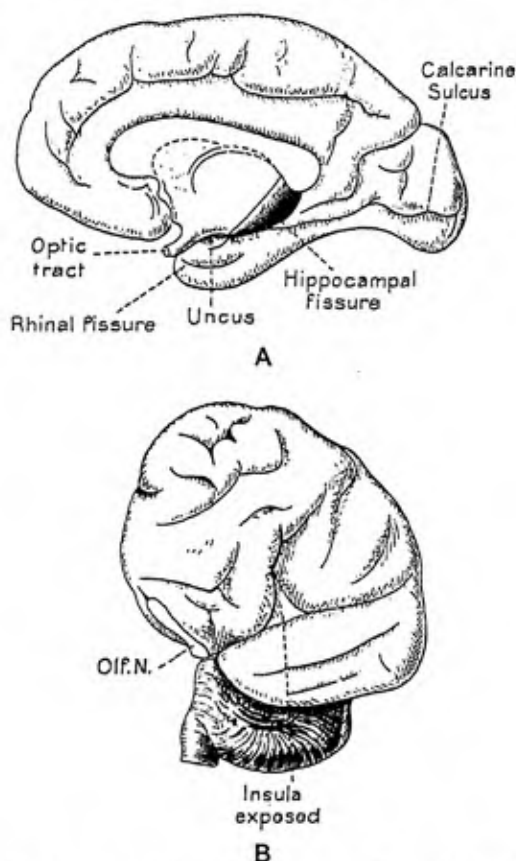


Fig. 124. Mesial (A) and frontal (B) aspects of the right and left cerebral hemispheres of a Gorilla (from a specimen in the Anatomy Museum at Munich). Note the very great similarity in appearance, as regards the mesial aspect, to the human cerebral hemisphere. The rhinal fissure (incisura temporalis) is conspicuous. In B note the uncovered state of the insula, and the lack of definite anterior limbs of the Fissure of Sylvius.

convexity (cf. Fig. 124 A)]. Nevertheless distinctions of importance remain, and some of these will now be considered briefly.

1. The Gorilla's brain is greatly inferior in point of size and weight. The human brain weighs about $2\frac{1}{2}$ times as much as

that of the Gorilla, and has therefore gained an accession of some 500 gm. of additional cerebral material.

2. In the adult Gorilla, the brain provides not more than $\frac{1}{150}$ part of the total weight of the animal, and may represent only $\frac{1}{200}$ part of that weight. The human brain provides about $\frac{1}{50}$ of the body-weight.

3. The extent of the neo-pallium has been remarked already as a distinctive character whereby the Primates may be ordained. The human brain possesses a vastly greater area of neo-pallium than that of the Gorilla. The estimates of this excess seem to vary somewhat. Thus one authority¹ states that in Man the neo-pallium has six times the area found in the highest ape, whereas data provided elsewhere² seem to indicate that the excess is represented by the figures 3·4 in the Chimpanzee, from which the Gorilla is not very different.

4. Taking a particular part of the neo-pallium, viz. the frontal area (Brodmann²) as a standard, it is claimed that this part provides 29% of the neo-pallial area in Man, while in the higher Simiidae, the ratio is but 17% (in the Cercopithecidae about 40%, in the Lemurs about 9%).

The consideration of these statements leads to such reflexions as the following:

(a) In point of size or mass of the whole body, Man and the Gorilla are sufficiently alike to exclude an appeal to the factor of size as the influential element in determining such differences. How important this may be in other cases, the study of small and large mammals of the same group or order will soon convince an investigator. It follows that the Gorilla's brain is to be regarded as shewing the amount and the surface-area requisite for the reception of the *general* sensory impulses arising from various parts of the surface of an animal nearly equal to Man in bulk.

(b) Another factor capable of determining an increase in the size or area of some part of the brain has been mentioned also in dealing with the lower forms. This is the particular development of one or other of the *special* senses, that of vision being especially

¹ Elliot Smith, *Rep. Brit. Ass. Dundee*, 1912. Section H. President's Address.

² Brodmann, *Anat. Anz.* 1912, and *Ergänzungsheft*, S. 211.

marked in the Lemurs. But so far as is known, Man possesses no marked superiority over the Gorilla in this respect, and it is probable that though the sense of hearing may be more acute in the ape, this does not greatly affect the comparison of the sense organs considered as a whole.

(c) Failure to provide an explanation by reference either to (a) general or (b) special sensibility, leads to an investigation of the motor mechanisms and more especially of the motor area of the neo-pallium. And herein relevant evidence is encountered. For the motor area of the neo-pallium exhibits a progressive increase in extent, culminating in the human cerebrum. It is to be noted, moreover, that this increased area marks an increase in the variety and range of movements, rather than an accession of strength. And the inferiority of even so highly developed an ape as the Gorilla in respect of skilled movements, such as those of the hands, confirms this assumption. Even more significant is the human superiority in the skilled movements of the lips, tongue, pharynx and laryngeal structures subservient to articulate language.

(d) The mysterious "association areas" of the neo-pallium remain for examination. These areas (neither purely motor nor sensory though in close touch with undoubted motor and sensory areas) have been identified in all the Primates described in the foregoing pages. In extent, they manifest a progressive development. In the brain of the Gorilla this has reached the latest stage so far known as antecedent to that found in Man. As a factor in determining the superior size of the human brain, the increase in the association areas is predominant over all others. The increase in extent affects not only the areas themselves, but certain outlying regions adjacent to them and to the areas of general and special sensibility.

A comparison of the brains of the Gorilla and Man may be drawn from the inspection of Figs. 125 and 126, in which the more important areas are indicated. In concluding this brief sketch of cerebral anatomy, two remarks may be added. Thus the figures just mentioned indicate a most suggestive relation between certain of the neo-pallial sulci and the *margins* or limits of some

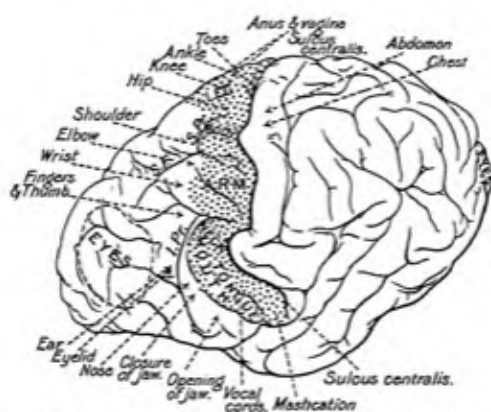


Fig. 125. Part of the cortical areas of the brain of Gorilla. (From Sherrington.)

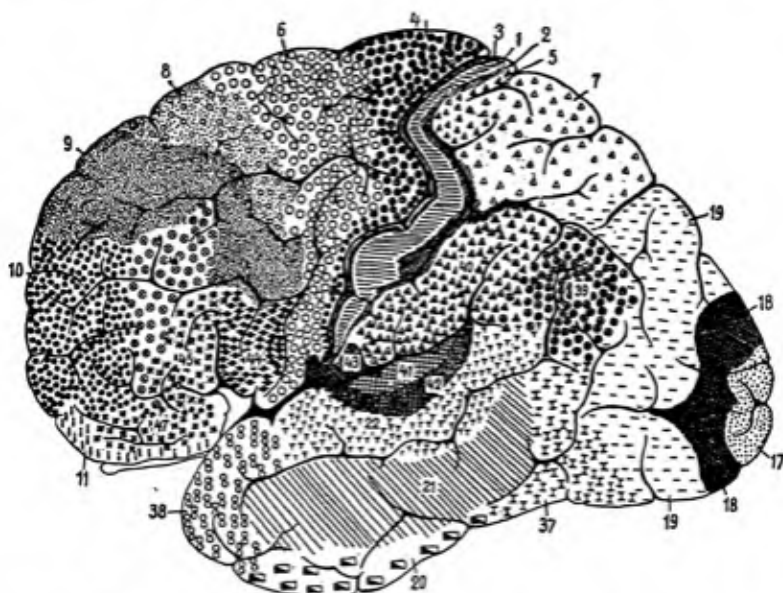


Fig. 126. Cortical areas of the brain of Man (from Brodmann, *op. cit.*). Note specially the areas marked 1, 4, and 17, and compare Fig. 125 with Figs. 46, 64, and 85. The areas specially mentioned are named as follows:—

- No. 1. Area post-centralis (sensory).
- No. 4. Area giganto-pyramidalis (motor).
- No. 17. Area striata (visual).

of the areas. Some sulci undoubtedly mark the boundaries of particular neo-pallial areas. And even though the precision and constancy of this relation be open to question, the general statement still holds good. On such grounds the significance of such furrows is greatly enhanced. Finally, the association areas, regarded in the light of their history, their disposition and their extent provide the best material basis so far known for the physical assessment of psychical differences between the ape and the human being.

The following notes provide an account of some details of the cerebral anatomy of the Gorilla.

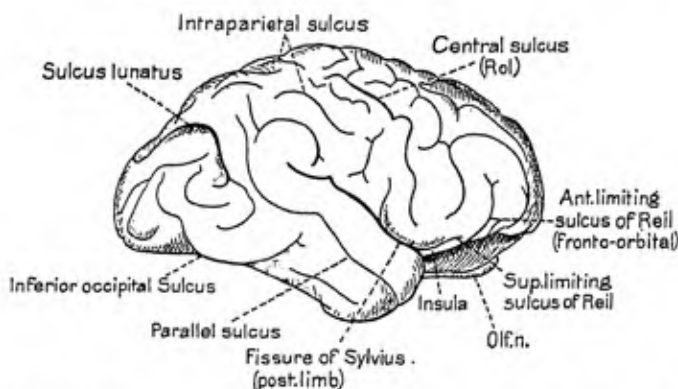


Fig. 127. Lateral aspect of the right cerebral hemisphere of a young Gorilla (*Simiidae*). The olfactory nerves are attenuated in point of size: the cerebral surface is much more convoluted than in the preceding examples and recalls the appearance of the human cerebrum. (Mus. Anat. Cant. Cr.)

When compared with the other large anthropoid apes, the Gorilla is seen to stand in a position nearer to Man than these. The cerebrum is ovoid, and strongly rostrated anteriorly, the frontal lobes being deeply excavated inferiorly by the upward projection of the orbital plates of the frontal bone. The frontal lobes are thus less full and rounded, both absolutely and proportionately, than those of Man. The occipital end of the hemisphere does not overlap the cerebellum to the same extent as in Man, and the cerebrum is smaller in proportion to the cerebellum than in the human brain.

The following notes are based upon Professor Elliot Smith's description of the brain of a Gorilla in the Museum of the Royal College of Surgeons. At the base of the brain the posterior rhinal fissure is retained with diagrammatic clearness, and thus demarcates the neo-pallium from the pyriform lobe. There is a deep vallecule Sylvii, which leads into the stem of the Sylvian fissure. The latter is formed by the meeting of temporal

and orbital opercula as in the human brain. As these opercula extend laterally they diverge, and expose a small triangular depressed area of insula. The orbital operculum is limited by a distinct fronto-orbital sulcus, which is really the anterior limiting sulcus of the insula. A dorsal opercular fold demarcates the lateral (superior) margin of the insula, and makes so complete a superior limiting fissure, that it appears to join the anterior limiting (fronto-orbital) sulcus, though closer examination reveals a strip of cortex dividing the two sulci. In most brains of Gorilla this strip is wide and quite easily seen. The mesial end of the fronto-orbital sulcus does not usually join the stem of the Sylvian fissure. The orbital surface of the frontal lobe is marked by a tri-radiate orbital sulcus to which smaller sulci may be accessory. The central sulcus presents a well-marked "genu." On the lateral surface of the frontal lobe, well-marked representatives of the sulci rectus and arcuatus are seen, and are evidently representative of the inferior frontal and inferior pre-central sulci of human anatomy. The superior pre-central and superior frontal sulci are arranged almost diagrammatically. A small sulcus frontalis medius and a representative of the sulcus fronto-marginalis (of Wernicke) may occur. The inferior transverse sulcus is commonly absent, but Eberstaller's sulcus diagonalis occurs.

The parallel sulcus is hooked round the extremity of the Sylvian fissure, much as it is in the Cynocephalous apes. The intra-parietal sulcus is clearly recognizable: the ramus post-centralis¹ superior is commonly independent of the last-named sulcus which dips posteriorly under the occipital operculum. The arcus occipitalis is very large, and wholly exposed, the mesial end of the occipital operculum having been pushed completely outward and backwards. A Y-shaped lateral occipital sulcus cuts into the occipital pole of the hemisphere. The occipital operculum is bounded by an almost semicircular Affenspalte.

The calcarine sulcus (cf. Fig. 128 A) consists of an anterior deep (true calcarine) portion, and a shallower retro-calcarine element, the latter being strongly inflected at its posterior end. A dorsal post-calcarine sulcus runs parallel to this last-mentioned portion.

The compound sulcus parieto-occipitalis of the mesial aspect is constant in occurrence, but very variable in extent and connections. The collateral sulcus may join the posterior element of the occipito-temporal sulcus, and operculation occurs in this region as it does in the genera Cynocephalus and Macacus. The calloso-marginal sulcus is very complete, and Broca's "compensatory" sulcus also occurs.

The cerebellum closely resembles that of Man. The floccular lobe however is larger than in human brains, and consists of two lobules each attached by its own stalk. The mesial lobule is much the larger and is

¹ The two sulci are continuous in the right cerebral hemisphere of a Gorilla preserved in the Anatomical Collection at Munich.

composed of three separate groups of folia whose separate peduncles unite in a common stalk. The lateral lobule is smaller and almost hidden by the former. It represents the flocculi secundarii of Man, which may correspond to the parafoeculus of lower mammals. The olivary body is in contact with

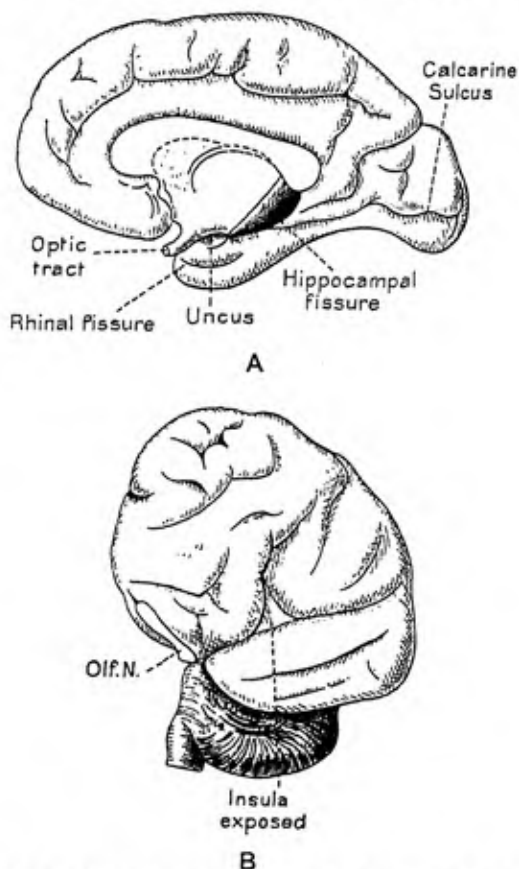


Fig. 128. Mesial (A) and frontal (B) aspects of the right and left cerebral hemispheres of a Gorilla (from a specimen in the Anatomy School at Munich). Note the very great similarity in appearance, as regards the mesial aspect, to the human cerebral hemisphere. The rhinal fissure (incisura temporalis) is conspicuous. In (B) note the uncovered state of the insula and the lack of definite anterior limbs of the fissure of Sylvius.

the lower margin of the pons. The trapezoid body is not exposed. The mesial geniculate body appears in some cases to be much more prominent than in Man (a prominence possibly associated with the larger size of the auditory nerve).

The study of the peripheral nervous system of the Gorilla falls naturally into two divisions.

(A) In the first place, a certain number of differences have been noted between the dispositions found in the Gorilla and in Man respectively, the differences affecting the course or connections of such nerves as are given in the following list (taken from Eisler's work¹).

The facial nerve is more complicated in the Gorilla than in the Chimpanzee, but less so than in the Orang-utan and in Man: its communications with the external carotid plexus are richer than in Man.

The ramus descendens hypoglossi contributes to the innervation of the sternomastoid muscle. The ansa hypoglossi receives branches from the first two cervical nerves. The great auricular and the superficial cervical nerves come from the second cervical only, the supra-clavicular from the second, third and fourth cervical nerves. The phrenic nerve contains sympathetic fibres. The nerve to the M. subclavius is not a distinct entity, since it arises from the uppermost (external) anterior thoracic nerve. The medial cutaneous nerve is derived principally from the first thoracic and intercosto-humeral branch of the second thoracic nerves. The musculo-cutaneous nerve receives no contribution from C. VII; it supplies the M. coraco-brachialis, but does not perforate it. The deep volar branch of the ulnar nerve springs from a communication between the ulnar and median nerves, and passes beneath the ligamentum carpi volare proprium to enter the hand. The median nerve passes beneath the M. pronator teres. The radial nerve does not perforate the M. supinator brevis.

The ilio-hypogastric and ilio-inguinal nerves arise from the thirteenth thoracic nerve, which is accordingly considered by Eisler as representative of the first lumbar nerve of Man. The femoral nerve receives most of its muscular fibres from L. IV. The anterior tibial (deep peroneal) nerve supplies (in correlation with the shifting fibula-wards of the dorsal interosseous muscles) the opposed surfaces of the second and third toes.

No contributions to the sciatic portion of the sacral plexus come from nerves posterior to the second sacral. The pudendal plexus is formed by the second and third sacral nerves, the coccygeal plexus by S. IV. and S. V.

(B) A second line of enquiry raises the question as to the relation of the general position of the limb-plexuses (as regards the spinal cord and its segments) in the Gorilla and other types. Here the first point to notice is that in one feature at least the Simiidae stand together with the Hominidae in contrast to all other Primates (save certain Semnopithecii). The feature thus

¹ *Das Gefäß- und periphere Nervensystem des Gorilla.* Exhaustive descriptions have been published also by Bolz, Kohlbrugge and Sperino.

distinguished consists in the presence of a contribution from the fourth cervical nerve to the brachial plexus. To this plexus, six segmental nerves contribute branches in the Hominidae, Simiidae (except the Orang-utan), and most Cercopithecidae, while the Platyrrhine apes and the Lemurs tend to possess a smaller representation (viz. from five segments only, and of these the fifth cervical is the most proximal in position). The Orang-utan in this respect stands apart from all other Primates, since no less than seven segments appear in its brachial plexus.

In the next place, and returning to the special study of the Gorilla, little direct evidence exists to shew that the great plexuses are definitely prefixed as compared with the conditions met with in Man. The evidence is in fact conflicting, and must so remain until a larger number of dissections has been made. Some suggestions of the prefixation of the cervical plexus in the Gorilla are furnished by records given in the preceding list (*v. section [A] supra*). In the brachial plexus, the median nerve receives a contribution from the fourth cervical segmental nerve and this record might also seem to point in the same direction. Otherwise the available data fall within the limits of human variation, and if the plexuses in Gorilla resemble the prefixed human types, yet they are not more prefixed than these.

Similar observations apply to the lumbar and sacral plexuses, but here a particular point demands attention. Thus in the survey of the lumbar plexus, if the nerve-roots contributing to such a nerve as the N. obturatorius be considered, it will be found that the segmental "thoraco-lumbar" roots of origin are alike in Man and the Gorilla, those numbered fourteen, fifteen and sixteen. But the Gorilla has commonly thirteen ribs, so that it is an open question whether its fourteenth nerve is the equivalent with the fourteenth in Man. If not, the obturator nerve in the Gorilla is derived (*inter alia*) from a segment nearer the last rib-bearing vertebra than is the case in Man, and it might be regarded in this manner as being prefixed. The view here taken is that the vertebrae are homologous "by numbers" regardless of the presence of ribs, and consequently no essential difference obtains between the Gorilla and Man in respect of the position of the lumbar plexus, or indeed of the sacral plexus.



Fig. 129.

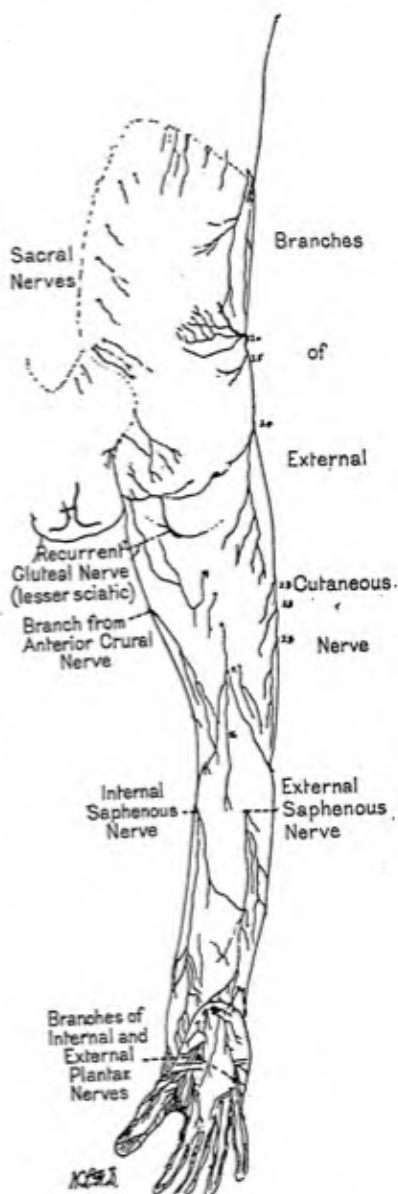


Fig. 130.

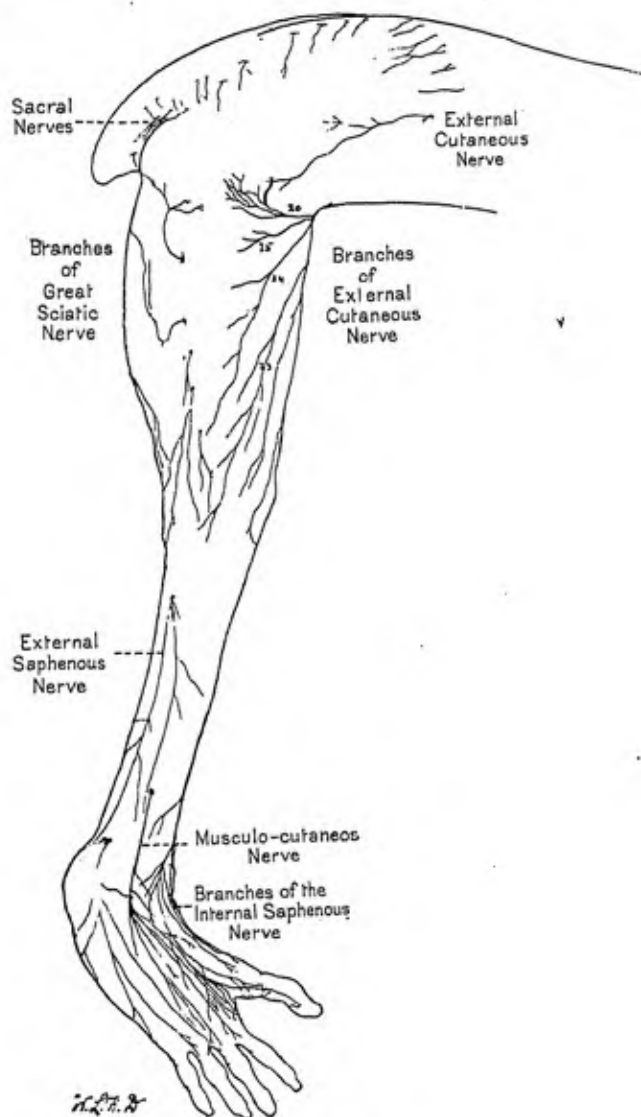


Fig. 131.

Figs. 129, 130, 131. Dissection of the lower limb of a Chimpanzee to shew the distribution of the cutaneous nerves. Note the lack of cutaneous fibres from the obturator nerve, and the absence of filaments from the anterior tibial nerve to the cleft between the hallux and first toe. (Mus. Anat. Cant.)

In the sympathetic chain three cervical ganglia are found, in addition to the ganglion stellatum; the second and third ganglia are placed more anteriorly than in Man. The sympathetic chain, the splanchnic nerves, and the vena hemiazygos pass together through the diaphragm. A ganglion meseraicum medium, not found in Man, lies between the aortic and coeliac plexuses. In many instances a single sympathetic ganglion is connected with two or more spinal nerves, and *vice versa* a single spinal nerve may send contributory fibres to two sympathetic ganglia.

The general distribution of cutaneous nerves to the lower limb of a Chimpanzee is shewn in the accompanying illustrations. (Figs. 129, 130, 131.)

I. Respiratory System. In an adult male Gorilla (specimen "Cy," Mus. Anat. Cant.) the hyoid bone is provided with a larger cornu majus than in Man. The basi-hyoid is excavated inferiorly, the cavity being sufficiently large to admit the tip of the little finger. (It is occupied by a diverticulum of the conjoined sacculi to be described presently.) The thyroid cartilage is rather smaller than its human representative, and thus stands in marked contrast to that of the Orang-utan. (The cricoid cartilage on the other hand is larger than in Man.) The superior thyroid cornu nearly touches the greater cornu of the hyoid bone.

The laryngeal pouches (cf. Fig. 121, *supra*) are of enormous extent. An appendix emerges over the superior border of the thyroid cartilage. After providing a large diverticulum towards the basis cranii, it becomes confluent with the sacculi of the opposite side and from this junction, an "infra-hyoid" diverticulum proceeds upwards to excavate the hyoid bone (Fig. 132).

The conjoined sacculi cover the larynx superficially and large symmetrical diverticula pass beneath the clavicles and pectoral muscles. An inter-pectoral diverticulum having been given off, the sacculi are finally traceable to the axillae. In females and in immature examples, the extent of these pouches falls considerably short of this, the arrangement in an adult male. As regards the function of these parts, we may accept provisionally the suggestion of Deniker, that the pouches serve the purpose not only of resonators for vocal efforts, but of supporting the lower jaw and parts of the head, and consequently of relieving the pressure of these weighty structures on the trachea.

The epiglottis is provided with a distinct hyo-epiglottideus muscle, suggestive of the arrangement found in the carnivora, but not normal in Man. No cuneiform cartilages were detected in the adult male example described, but the cornicula were large, and gave a recurved appearance to the arytenoid cartilages.

The plica vocalis ("true" vocal cord) when viewed in coronal section, exhibits an attenuated membranous flange at its free margin (Fig. 133). The M. thyro-arytenoideus has a distinctly

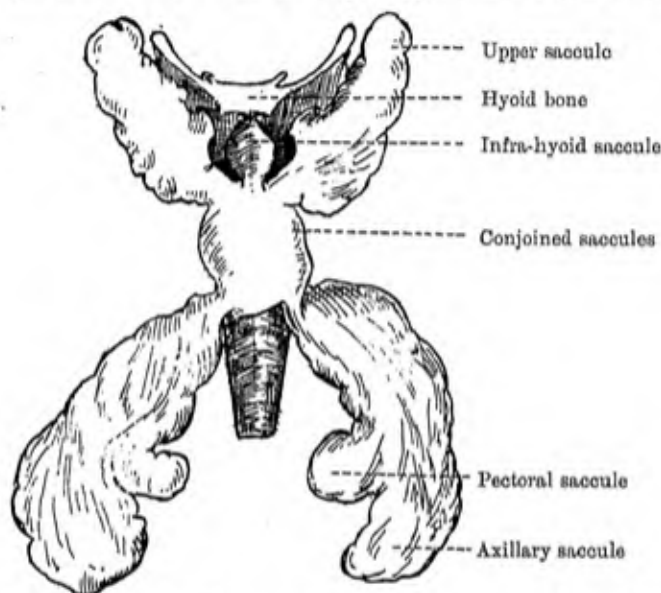


Fig. 132. Diagram of the laryngeal pouches of an adult male Gorilla (Specimen "Cy," Mus. Anat. Cant.). Communication with the laryngeal cavity is established on each side (laterally but not medially) near the base of the "upper sacculo" and just below the level of the hyoid bone. Thus the two lateral out-growths have evidently coalesced as the "conjoined sacculo."

circumscribed outline. In these characters (of the plica vocalis) a contrast with the human larynx is distinct, and though the Gorilla has advanced beyond the stage reached by the Cercopithecidae, yet the Chinpanzee and not the Gorilla makes the nearer approach to Man in such details.

The thyroid body consists of two lateral lobes (about the size of large almonds) joined by a narrow isthmus. No pyramidal lobe was seen in the animal dissected by me.



Fig. 133. Gorilla (adult male). Coronal section through middle third of plica vocalis. Two or three "nests" of muscle-fibres are seen (M) in the plica ventricularis. No isolated muscle-fibres in the plica vocalis. ($\times 7$ approximately.)

The pleurae have been minutely described by Ruge¹. As regards their caudal extension along the vertebral column, some approach to the human condition is seen, for the lower limit here is above rather than below the last rib (the latter may however be the thirteenth or fourteenth). Anteriorly (ventrally) Ruge noted a wide interval between the margins of the two pleurae in the sterno-costal region, and in this detail, the Gorilla may be con-



Fig. 184. An adult male Orang-utan (from a sketch by M. Millot, reproduced with permission from the proprietors of *L'illustration*).

sidered to depart further from the lower Primate type than does Man himself. Laterally the line along which the lower limit of the pleura recedes is closely comparable to its human counterpart. The sub-pericardial sinus (formed by the mediastinal pleura) is retrogressive, though it may co-exist with a small lobus azygos of the right lung.

¹ In the *Morphologisches Jahrbuch*, Band xix.

The division of the lungs offers no points of contrast with the human type, though the Orang-utan is completely aberrant, viz. in the absence of all divisions. In the Gorilla, the lobus azygos is occasionally present.

Here the thymus may be mentioned. It is said to be voluminous in the foetus at the fifth month, but its disappearance seems to be more rapid than in Man.

J. Alimentary Canal. The lips of the Simiidae are very mobile as may be judged from the lifelike sketch by M. Millot, reproduced as Fig. 134. But the effect is somewhat masked by the thickness of the lips and their incomplete eversion (Fig. 135). In such respects the Simiidae still resemble the Cercopithecidae, even though a slight advance may be noted in the disposition of the orbicular muscle-fibres.

The tongue is long and narrow (Fig. 136), the relation of its width to its length being as 1 to 3.6 (Ehlers). Thus it is strongly contrasted with the human tongue, and the contrast is enhanced by the remarkable filiform papillae (Fig. 137) near the root. The tongue of the Chimpanzee (Fig. 138) approaches that of Man much more nearly in these characters.

In the tongue of the Gorilla, five circumvallate papillae were observed by me, but the precise position of the foramen caecum was obscured. The tonsils are well developed and in general the superior laryngeal aperture may be said to resemble that of Man or of the Chimpanzee, while the corresponding region in a large adult Orang-utan provides an extraordinary contrast with all the preceding examples (Fig. 139).

On the ventral aspect of the tongue, a lingual fraenum recalls the corresponding fold in the human mouth. Two other folds are situated symmetrically, one on each side of the fraenum, but I cannot identify these definitely with the plicae fimbriatae. Palatal rugae are well marked.



Fig. 135. Sections of upper and lower lips of a young Gorilla. (Mus. Anat. Cant.)



Fig. 136. Tongue and superior laryngeal aperture of adult male Gorilla.
(Specimen "Cy," Mus. Anat. Cant.)



Fig. 137. Superior laryngeal aperture, and (below it) filiform and circumvallate papillae of the tongue of an adult male Gorilla. (Specimen "Cy," Mus. Anat. Cant.)



Fig. 138. Tongue and superior laryngeal aperture of a young Chimpanzee.
(Mus. Anat. Cant.)

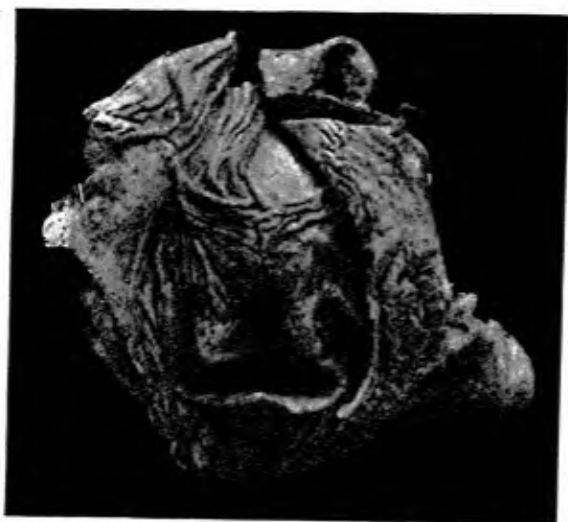


Fig. 139. Superior laryngeal aperture of an adult male Orang-utan. (Specimen
M.C.H., Mus. Anat. Cant.) To be contrasted with Fig. 137.

The stomach is a simple sac, having relations similar on the whole to those of the human stomach, with the exception that as regards the transverse colon the human stomach is higher, that of the Gorilla being often lower and thus rather behind than above the transverse colon. In the adult Gorilla the human arrangement may however obtain. (Cf. Fig. 140.)

The small intestine is quite distinct in appearance from the large: the relative lengths of these two portions of the gut vary

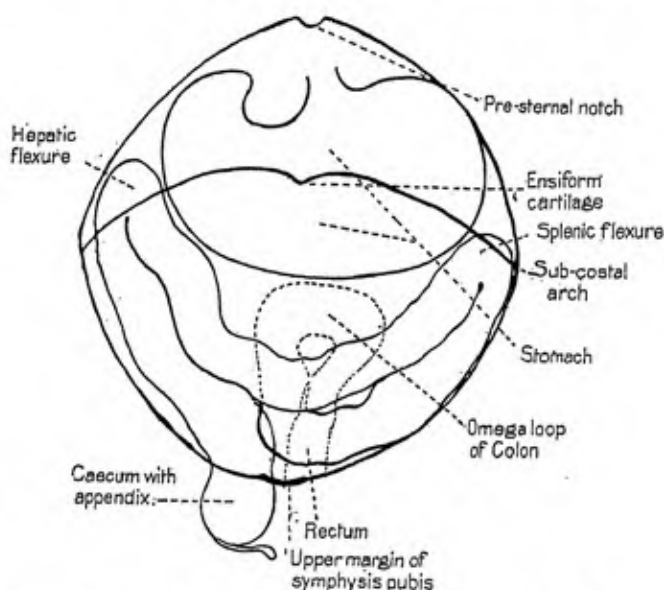


Fig. 140. Diagram (to scale) of the relations of the stomach and large intestine in an adult male Gorilla ("Cy"). The stomach is fully distended in this specimen.

in the following way; in a foetus of 5 months the length of the small intestine was to that of the large intestine as 3 to 1; in a young Gorilla the proportion 4.8 to 1 has been found, and in an adult Gorilla the proportion of 2.1 to 1 obtained. There would thus appear to be irregularity in the rate of growth of each portion of the gut, and the irregularity is of a reciprocal kind. The general characters of the intestine do not differ materially from those of the human intestine. Deniker suggests that in the Gorilla the vermiform appendix caeci increases in relative size

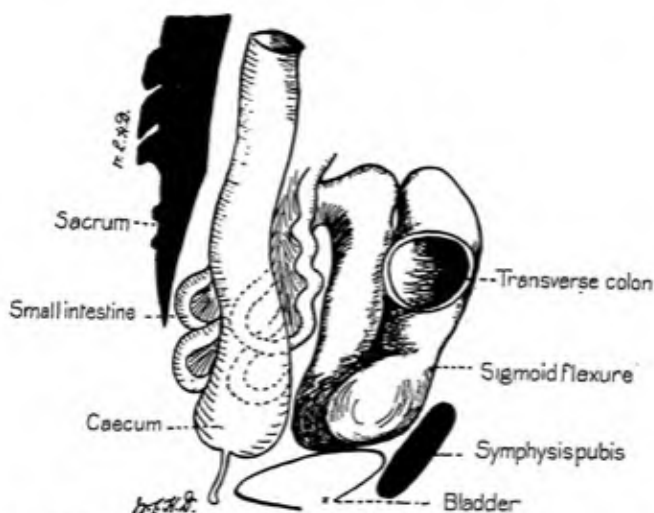


Fig. 141. Abdominal and pelvic viscera of an adult male Gorilla, seen from the right side. Note the extent to which the caecum and appendix have descended into the pelvic cavity. (Specimen "Cy"; Mus. Anat. Cant.)

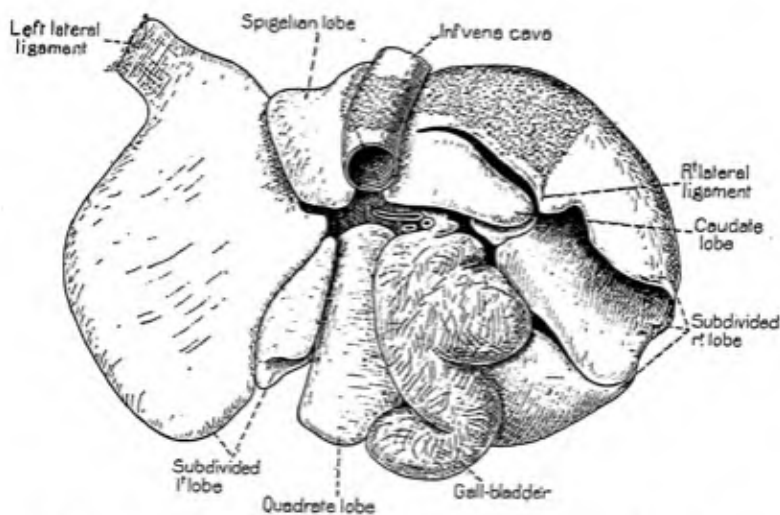


Fig. 142. Visceral aspect of the Liver of a young Gorilla. (Mus. Anat. Cant.)

with the age of the animal, whereas it decreases with age in Man. For the position of the caecum cf. Figs. 140 and 141.

The pancreas does not differ apparently from that of Man: the characters of the spleen however are distinctive, the most striking being the extreme attenuation of this organ in its lower parts, so that its extremity is tapering and caudiform, suggesting the conditions obtaining in the lower Anthroidea and in the Lemurs.

The liver of the Gorilla (cf. Fig. 142; the inferior aspect of the liver of a young Gorilla is represented) differs from those of the other large anthropoids and of Man in the more marked tendency to subdivision of right and left lobes, a character which assigns a comparatively lowly place to the Gorilla in a comparison of the higher Primates based on the anatomy of the liver.

The general relations of the peritoneum are the same as those of Man.

K. Genito-urinary System. The genito-urinary system offers no important differences from that of Man.

The kidneys may present but a single pyramid as in *Hylobates*, but this is a variable character in Gorilla. The genitalia of the female differ in arrangement from the human type, inasmuch as the vulva is directed posteriorly. The vagina, uterus, Fallopian tubes, and ovaries resemble the human organs. The existence of a hymen is denied by various observers: this membrane would thus appear to characterize the Hominidae alone among the Primates.

In the male, the glans penis is smaller relatively and absolutely than that of Man, but is nevertheless more distinct and relatively larger than in other Simiidae. There is an os penis, as in the lower Primates, and other Eutherian mammals. The Hominidae alone amongst Primates would seem to be characterized by its absence.

In an adult male Gorilla I found the tunica vaginalis of the left testis completely free from all connection with a processus vaginalis. The cavity of the tunica vaginalis was distinctly smaller than in Man and in the Chimpanzee. A pedunculated hydatid was present. The testis measured 51 mm. in its longer axis. In an adult male Chimpanzee, the right testis

measured 51 mm. by 26 mm. The tunica vaginalis bounded a closed sac. No hydatids were seen. The epididymis was placed as in Man but on its dorsal aspect a large accumulation of fatty tissue was noticed.

Professor Retzius very kindly reported on the two testes described above. That of the Gorilla was imperfectly preserved, but the testis of the Chimpanzee provided well-preserved sperm-cells. The characters of these are mentioned in the following paragraphs.

The spermatozoa of the Gorilla have been described by Professor Retzius¹, who has illustrated his admirable observations in several well-known memoirs.

The sperm-cells possess distinctive features in each of the larger Simiidae, and while the Orang-utan is quite aberrant in these respects, the Chimpanzee and the Gorilla must be placed much closer to Man in regard to such characters.

(a) In the spermatozoa of the Gorilla (Fig. 143, No. 7) the head is of ovoid form, though flattened in one plane: when viewed in the flattened aspect, the acrosome (perforatorium) is seen to be more slender towards its free extremity than in the Chimpanzee. In this respect the Gorilla is of all the Primates the form most similar to Man.

(b) The pars conjunctionis of the tail (with the included centrosomes) is relatively shorter in the Gorilla than in the other Simiidae, and herein again the human conditions are most nearly approached by the Gorilla. (It may be added that a small New-World monkey, viz. *Callithrix*, and the *Hylobates* resemble Man and the Gorilla in this detail.)

(c) The pars principalis of the tail is (in the sperm-cell of the Gorilla) slender and of moderate length. Again the Gorilla makes the closest approach to the condition found in Man.

This survey of the main characters of the Simiidae shews their close similarity to the Hominidae: at the same time differences as well as resemblances are indicated, differences chiefly noticeable in two connections, viz. with the adaptation of Man to the erect attitude, and secondly, with the concomitant development of brain-

¹ Retzius, *Biologische Untersuchungen*, N.F. Bd. xvii. 1912 and *Anat. Anz.* 1913.

mass and function. These two principles are closely allied, and the mode of adaptation of the Primate type to an erect position, and

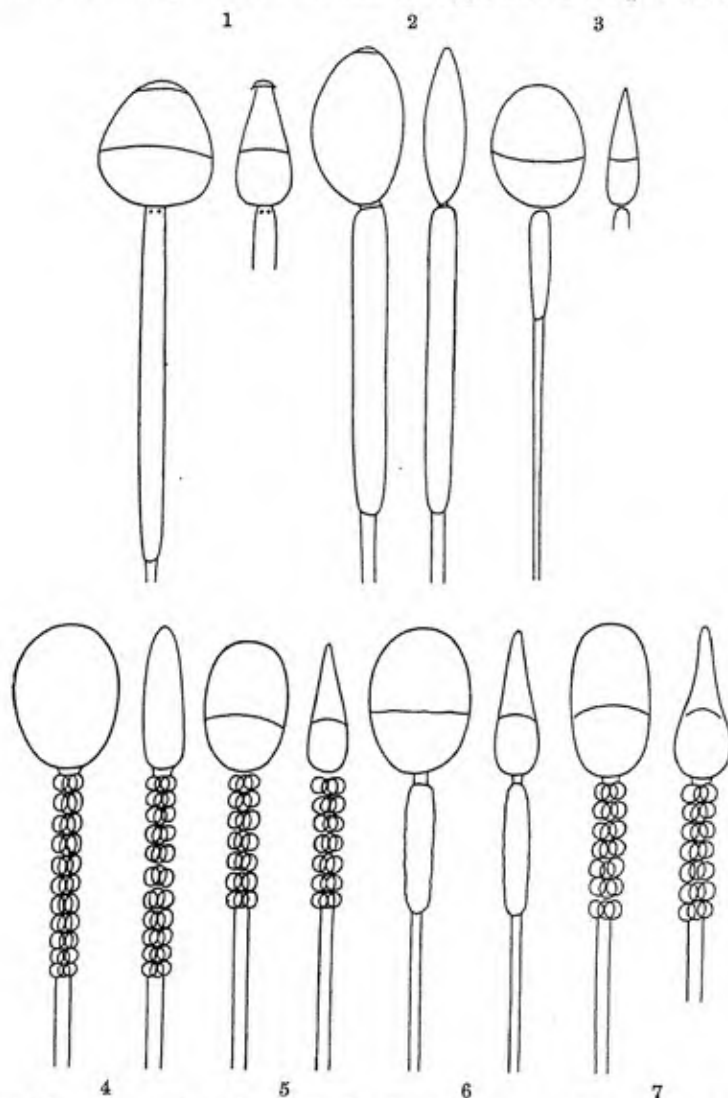


Fig. 143. Sperm-cells of the Gorilla (No. 7) and other apes. For references see Fig. 51. (After Retzius, *op. cit.*)

the characters attendant on the greater cerebral development will be considered in some of the ensuing chapters.

CHAPTER V

THE CRANIA OF THE SIMIIDAE (PRIMATES)¹

HAVING completed a general account of the anatomy of selected types of the Primates, we turn to the cranial characters of the Simiidae in particular; and inasmuch as the skull of Gorilla has already been described, this form will demand less attention here than the remaining members of the family, viz. the Gibbons, Orang-utans and Chimpanzees. To the first of these, the Gibbons, we may now turn, taking as our examples skulls of animals of the Bornean variety known as Müller's Gibbon (*Hylobates mülleri*), and proceed to consider the points laid down in the accompanying list.

I. Cranial portion:

General contour.

Sutures.

Ridges.

II. Facial portion:

Orbit: General contour and margins.

Lachrymo-ethmoidal suture.

Lachrymal hamulus.

Infra-orbital suture.

Nasal aperture:

General contour.

Lower margins.

Nasal spine.

Nasal bones.

¹ For further details, the exhaustive paper by Dr Stefanie Oppenheim should be consulted. Cf. *Z. f. M. und A.*, Band xiv. 1911, *Zur Typologie des Primaten-craniums*.

- Palate: General contour.
 Post-palatine spine.
 Tuber maxillare.
 Palatine sutures.
- III. The Temporal Fossa:
 Sutures at pterion.
 Depth of fossa.
 Post-orbital wall.
- IV. Base of the skull: Glenoid fossa.
 Endoglenoid tubercle.
 Margin of foramen magnum.
 Styloid process.
- V. Dentition: Number of teeth.
 Characters of teeth.
- VI. Mandible.

CRANIAL CHARACTERS OF HYLOBATES MÜLLERI

As is to be expected from the smaller size of the animal, the skull (Fig. 144) is much less bulky than that of the Gorilla (or indeed of the other Simiidae): in length the brain-case (cranium) will be found to measure about 75 mm.,

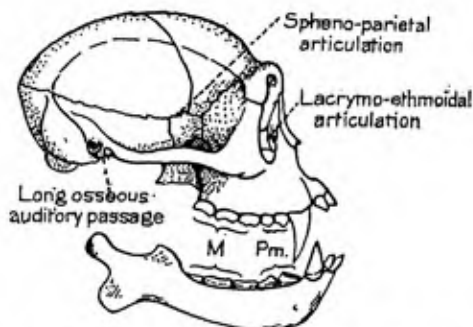


Fig. 144. Cranium (with mandible) of *Hylobates mülleri*: note the absence of an auditory bulla; there are spheno-parietal and lacrymo-ethmoidal articulations. Note also the number of the teeth. (Hose donation II; Mus. Anat. Cant.)

whereas in the larger animals of this family twice that figure would represent the corresponding dimension.

In size and in general appearance the skull resembles those of the higher Cercopithecidae rather than those of the Simiidae. By way of distinction

from the former (the Cercopithecidae) the following points may be mentioned. Thus in the *Hylobates* the brain-case is proportionately larger in comparison with the facial skeleton, the contour is ovoid, the surface of the cranium is devoid of prominent crests, though the outline of the area occupied by the temporal muscle is shown by an upraised linear ridge. The cranial capacity varies from 76 c.c. to 90 c.c. in this species and the sexual difference is very small (Oppenheim). The sutures demand no special mention. The orbital cavities are remarkably capacious. The latter feature is associated with the small size of the animal, in accordance with a general law as to the proportions subsisting between the animal's absolute bulk and the size of the eyes. This feature modifies the appearance of post-orbital lateral compression (of the skull), which is really present.

Turning now to other facial characters, it will be seen that the orbital margins are distinct or trenchant, that the lachrymal hamulus is vestigial, that the os planum of the ethmoid is not infrequently divided into anterior and posterior portions, and that the sphenomaxillary fissure is widely open. The infra-orbital suture does not persist on the facial aspect. The nasal aperture has an ovoid form or contour, with margins which are obliterated inferiorly. No nasal spine is seen: the nasal bones are early conjoined by synostosis, and the compound bone has a somewhat quadrate contour and is flat, not suggesting the prominence of the soft parts of the nose. The palate is hypsilloid (U-shaped) in contour, with a diminutive posterior spine: the tuber maxillare is also diminutive. In the region of the temporal fossa the rudimentary character of the alisphenoid (as compared with its condition in Man) is at once seen: this bone joins the parietal at the pterion: and the infra-temporal crest is insignificant.

At the base of the skull the shallowness of the glenoid fossa arrests attention. Yet this shallowness cannot be taken to indicate much freedom of the mandible in lateral movements. For the large canine teeth limit such movements very considerably and markedly. No endoglenoid tubercle is developed as in the Gorilla, though a post-glenoid process is distinct. Styloid and vaginal processes are not seen.

The dentition provides the normal formula for Catarrhine Primates. The canines greatly exceed the neighbouring teeth in size: the molars are tetracuspoid and the talon in the lower molars is not conspicuous.

The mandible is characterized by the shortness of the ascending ramus, by the projection of the angle and by the absence of genial tubercles. The vertical height of the body of the jaw in the region of the second molar tooth is much less than the height at the first premolar tooth. Near the latter, the jaw is deep and massive, and the same remark applies to the region in which are implanted the incisor and canine teeth. Such an increase in strength is related to the large size of the canine teeth, and it reproduces the condition exhibited in an even more pronounced degree by the extinct cat named *Pogonodon* (Cope).

CRANIAL CHARACTERS OF *SIMIA SATYRUS*¹.

The researches of the late Professor Selenka of Munich led him to distinguish some seventeen different varieties of Orang-utans, most of which might be regarded as constituting distinct though local races. Many writers before Selenka had urged the necessity of recognizing marked distinctions between specimens derived

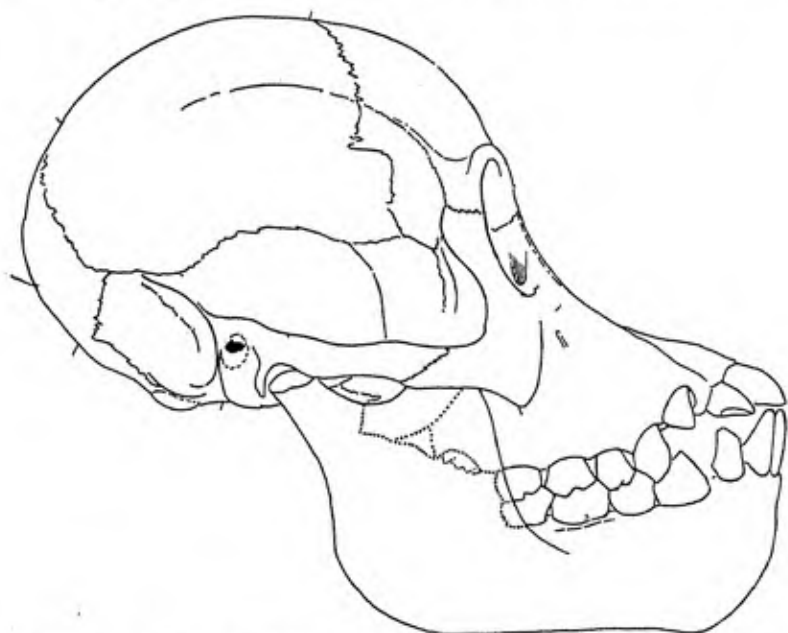


Fig. 145. Cranium (with mandible) of an Orang-utan (Mus. Anat. Cant.); note the absolute obliteration of nasal prominence, the absence of an auditory bulla, the presence of a sphenoparietal articulation, and the number of the teeth. The lacrimal and ethmoid bones join on the inner orbital wall with separation of the frontal bone and maxilla. ($\frac{1}{3}$ nat. size.)

from various localities. The memoir by Fitzinger, published in 1854, is by no means the earliest on record, but it provides an excellent account of the literature of the subject up to that date. The accounts thus accessible will be found to deal with the external appearance and also with the cranial characters of the Orang-utan. Fitzinger's work is of interest here, since the author lays special

¹ For the revised nomenclature v. *supra*, p. 153, footnote.

stress upon the differences observed in the profile of the face in various examples. Thus it was noticed that some crania present a straight facial outline, the flattening of the nose having been carried to this extreme. But a second type surpasses even the former in this respect, for the profile is so to speak "concave" or hollowed-out as Fitzinger describes it. The accompanying illustration (Fig. 145) shews a cranium with a moderately hollowed-out profile. To this type, the epithet *simognathic* was given by Selenka, and more recently (1913) Keith applied the term *simoprosopic* to the same condition, regarding it as generally distinctive of the Orang-utan in contrast with the other Simiidae. Keith's contribution to this subject is of great importance, for he shews that in respect of its facial conformation, the Orang-utan has experienced a change analogous to, if not identical with, that distinguishing the bull-dog from the more normal canine varieties. And further, it is claimed that the defective growth of bone may induce a similar condition in the human skull, in which it has been long known as Achondroplasia. Several other illustrations will be added in the sequel. Here it will suffice to note that even though not all crania of Orang-utans are strictly *simognathic*, yet all tend to this condition, which is so distinctive as to provide a most ready means of identifying the crania of this genus of the Simiidae.

Taking for descriptive purposes a young individual on the verge of maturity we remark at once the great increase in size upon that of the *Hylobates* skulls. The proportions too of face and cranium are different, the facial part having gained in bulk; to this gain a notable contribution is made by the mandible.

In proportions, the cranial part of the skull is, when contrasted with the facial part, less elongated than in *Hylobates*, and presents the nearest approach to brachycephalic proportions (cf. Chapter XI) met with among the Simiidae. The cranial capacity ranges from 355 c.c. to 540 c.c. in adult males, and from 300 c.c. to 490 c.c. in females (Hrdlička)¹. The cranial sutures early become simplified and are closed by synostosis. Traces of the division of the parietal bone into upper and lower halves are stated by Ranke to be very frequent (the trace consisting in a remnant of the dividing suture persistent at its starting point from the coronal suture).

Rapidly converging from the external angular processes of the frontal bone, the temporal ridges vary in their ultimate conformation, the sexual factor being

¹ *Proc. United States National Museum*, Vol. xxxi. p. 544.

of importance. For in the female Orang-utan the ridges may remain separated throughout their course, or may barely come into contact with one another, whereas in the male animal, not only may the ridges meet, but they may rise in the form of a crest measuring as much as 10 mm. in height. Posteriorly, the temporal ridges vary too, in male examples meeting the superior nuchal line, and forming a lambdoid crest not seen in female skulls.

The orbits have an elliptical contour, and the brow ridges are not (as in the African Simiidae) continuous from side to side of the forehead. They are also stouter laterally than medially. The orbital margins are distinct; the lachrymal hamulus vestigial, but there is an elongated lachrymo-ethmoidal suture, since the os planum of the ethmoid though of small vertical extent is somewhat higher anteriorly than elsewhere.

The spheno-maxillary fissure is a mere cleft of small dimensions, the post-orbital wall being in consequence almost complete. The infra-orbital suture rarely persists long on the facial surface. The nasal aperture is pyriform with upwardly directed apex: inferiorly the nasal margins are quite lost, and no nasal spine is seen, though in some cases it is represented by a median ridge. The nasal bones are more reduced in size than in any other Primate mammal; usually the conjoined bones form a mere elongated splint, and not infrequently no distinct nasal bones remain: sometimes a small ossicle at the upper margin of the nasal aperture is all that persists; the nasal processes of the maxillae then join each other between the orbits.

The palate is elongated and hypsiloid: the tuber maxillare is variable in development, as is also the post-palatine spine.

The temporal fossa is deep, owing to the bowing outwards of the zygomatic arch and the channelling of the alisphenoid. The latter bone touches the parietal, and thus the Orang-utan agrees with Hylobates, Man, and many lower Primates, but differs from the African Simiidae and most of the Catarrhine monkeys: the variations in human skulls in this respect will be described in a subsequent chapter.

The infra-temporal crest is insignificant. At the base of the skull the shallowness of the glenoid fossa is to be remarked, but as was noted in describing the cranium of Hylobates, this shallowness is not to be regarded as related to lateral movements of the mandible, which are limited by the excessive development of the canine teeth. Movements in an antero-posterior direction may possibly occur and may produce some effect as regards the glenoid surface. The endoglenoid process or tubercle is small, as is the styloid process, which is often absent. The vaginal process is also undeveloped. Anomalies about the margin of the foramen magnum are not common, though the ossification of the adjacent part of the suspensory ligament sometimes leaves a spicule of bone at the anterior margin. As regards the endocranium, a distinction between the Orang-utan and the two African Simiidae was pointed out by Huxley. In the Orang-utan the cribriform plate of the ethmoid articulates posteriorly with the pre-sphenoid, as in Man. In the Chimpanzee and Gorilla these two bones are separated superficially by flange-

like processes growing from the frontal bone on each side and meeting in the middle line. In this disposition we encounter a rare occurrence, viz. the encroachment of the membrane-bones of the skull upon the territory of this *basis cranii*. The principal points of importance in the mandible are its very massive character in proportion to the rest of the skull; the ascending ramus, which is higher than in *Hylobates*, and which bears a shallow sigmoid notch. But in fact the mandible is found to present several distinct variations. Thus the relative height of the ascending ramus is by no means constant: the lower margin of the body of the jaw may be rectilinear, sinuous, or uniformly curved. Consequently some of the mandibular types described as distinctive of certain varieties of Man may be shewn to possess counterparts in the jaw of the Orang-utan.

The teeth provide the normal formula, but in males accessory molar teeth are extremely common. The great length of the roots of all the teeth is noticed by Tomes (*Dental Anatomy*) as peculiar: also the curious crenation of the enamel (which, though a feature of the developing tooth, persists in the crowns of the molars of the Orang-utan) is remarkable. The third molar tooth in the upper jaw tends to smaller dimensions than the other two.

CRANIAL CHARACTERS OF ANTHROPOPITHECUS NIGER.

There remain to be enumerated the cranial characters of the Chimpanzee (*Anthropopithecus niger*). It may be pointed out that this ape and the Gorilla agree in several important respects wherein they both differ from the Orang-utan. This general statement applies to the skull as well as to other anatomical structures.

Taking as our example a young, but nearly mature, individual (Fig. 146), we notice that, viewed from above, the skull of the Chimpanzee is more ovoid in form than that of the Orang-utan. The facial skeleton is rather smaller in proportion to the cranial part than in either the Orang-utan or the Gorilla, and here in the Chimpanzee skull (especially in infancy, cf. Fig. 147) suggests the proportions of the human skull, though it is still far from realizing them.

The cranial capacity of adult males provides an average value of about 400 c.c. (Oppenheim, *op. cit.* p. 138 gives 404.3 c.c.) with a maximum of 470 c.c. The adult female skull is less capacious and amounts to about 95 % of that for the male. The instructive table drawn up by Oppenheim is reproduced here in order to exhibit the sexual variability in several of the

Primates. Thus the female cranium in all instances is smaller, and the percentage values in terms of the male capacity (taken as 100) are as follows:

Cynocephalus	83
Hylobates	98
Orang-utan	90
Gorilla	85
Chimpanzee	95



Fig. 146. Cranium of adult female Chimpanzee (Mus. Anat. Cant.). One-third of natural size.

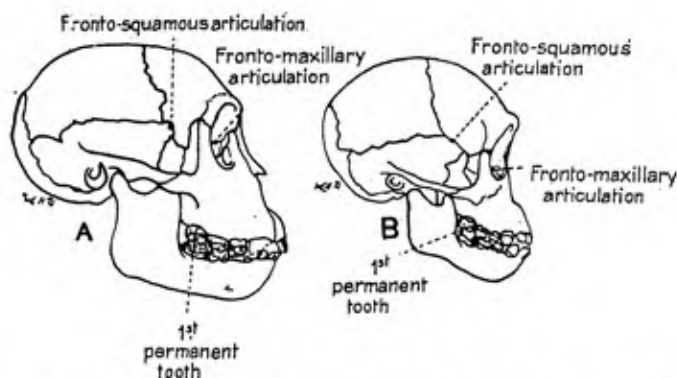


Fig. 147. Crania, with mandibles, of (A), young Gorilla, and (B) young Chimpanzee (Simiidae). The first permanent tooth (the first molar) has just been fully acquired in each case, and comparisons can thus be drawn between examples at corresponding stages in development. Note the greater nasal prominence in the Gorilla; and the fronto-squamous and the fronto-maxillary (orbital) articulations in both specimens.

Of the cranial sutures, the sagittal may be extremely complicated and tortuous before it becomes closed; on the other hand, the straight outline

of the suture dividing the parietal bone from the squamous portion of the temporal bone is to be noted.

Bony crests occur on the surface of the cranium, but are comparable rather to those of the Orang-utan than to those of the Gorilla. For it is the exception rather than the rule for the temporal ridges to form a median sagittal crest: they commonly run in close approximation along the sagittal suture, diverging thence with the formation of lateral lambdoid crests.

The contour of the orbit is less definitely elliptical than in the Orang-utan, and herein the Chimpanzee and Gorilla resemble one another; similar agreement between the two African apes is seen in the prominence of the external angular processes of the frontal bone, in the continuity of the supra-orbital ridge between these two processes and across the inter-orbital space, in the bevelling of the external orbital margin, and in the shortness of the lachrymo-ethmoidal suture. The lachrymal hamulus is vestigial, and the sphenomaxillary fissure reduced to a narrow cleft.

The nasal aperture is pyriform, with the truncated apex above; the lower margins of the aperture are obliterated, and no nasal spine is seen. The nasal bones are often conjoined at an early epoch, and their flat expanse is not relieved by the very remarkable median ridge so characteristic of these bones in the Gorilla. The nasal bones preserve a more uniform breadth from above downwards than in the Gorilla, and do not extend so far below the level of the lower orbital margins as in the latter animal.

In the development of frontal air-sinuses, and of similar air-cavities in the ethmoid bone, with dilation of the nasal duct, where this is in relation with the maxillary antrum, the Chimpanzee and Gorilla agree, and approximate to the human condition (cf. Keith, *Proc. Anat. Soc.*, 1902), while they differ herein from the Orang-utan and Gibbon.

The maxillary antrum is of smaller extent, both absolutely and relatively, in the Chimpanzee than in the Gorilla. The reduction affects all parts of the antrum, but sometimes the upper and hinder portion is particularly diminished. In such instances I have noticed that the foramen rotundum is visible when the orbital cavity is viewed from in front. But this is by no means always the case in the Chimpanzee. I may add that the foramen rotundum is thus visible usually in the Cebidae, and occasionally in the Cercopithecidae. Once only have I seen this condition in a human skull, viz. that of an African negro dissected in the Cambridge Anatomy School. But inflation of the antrum is by no means the only factor involved in this matter, which cannot be pursued further in this place. The palate has the characteristic simian hypsiloid contour, and the post-palatine spine is small, as is also the tuber maxillare. The maxillary antrum is said to extend into the palatine portions of the maxillae. Great irregularity of the arrangement of the palatine sutures is frequent.

The temporal fossa owes its depth largely to the channelling of the alisphenoid, which commonly articulates with the frontal and squamosal

above, being separated by these two bones, which join at the pterion. The infra-temporal crest is often represented by a single spinous process.

The base of the skull shews the foramen magnum in the position characteristic of Simiidae, i.e. much nearer the occipital end of the skull than in the Hominidae. The glenoid fossa is shallow, with a moderately developed endo-glenoid tubercle, and small post-glenoid process. As in the Gorilla, an Eustachian spinous process is common, but the styloid and vaginal processes are absent. The tympanic bone, as in the other Simiidae, is extensive from without inwards and semi-cylindrical in form. The occipital condyles are small and variations in the conformation of the margins of the foramen magnum are rare.

The mandible is smaller and weaker than in the Orang-utan or the Gorilla, but still massive in comparison with the human jaw. The area for the digestive muscle (anterior belly) is a narrow strip or (in many cases) not to be identified. Posteriorly to the symphysis in the middle line is a deep pit, and at the lower margin of this, neither a ridge nor tubercles are found.

The dentition presents the usual Catarrhine formula: the canine teeth, except in old males, do not so far surpass the other teeth in bulk, as in Simia and Gorilla. Yet the canines are of very great size in comparison with those of Man, and this is the more remarkable when it is remembered that the molar teeth, in male skulls with such large canines, may fail to attain the dimensions even of European molars. These considerations are of great importance in the study of prehistoric mandibles such as those from Mauer and Piltdown.

The diastema is less wide in the Chimpanzee than in the other Simiidae. In the reduced size of the third upper molar teeth, and in the small cusps of the molar series, anticipations of the human conditions are present. Slight but distinct crenation of the crowns of the molar teeth frequently occurs.

In concluding these brief descriptions of the external characters of the skulls of Simiidae, it is convenient to present the main points of diagnosis of the several genera in a tabular form as follows:

Distinctive features of the skulls of Simiidae.

I. *Hylobates* (Gibbon).

Its small size differentiates it from those of other Simiidae. The skulls of Cercopithecidae of similar size are distinguished by their relatively smaller capacity and by the nasal bones (which are longer than in *Hylobates*). The molar teeth of *Hylobates* do not possess the two transverse ridges crossing the crown which are so characteristic of the teeth of the lower Anthropoidea.

II. *Simia* (Orang-utan).

Distinguished by its absolute size from the skull of *Hylobates*.

Distinctions from Chimpanzee and Gorilla:

(a) The supra-orbital ridge for each orbit is distinct and the two ridges are not continuous across the forehead.

(b) The nasal bones are reduced to mere splints. The facial profile is often concave (simognathic), and though some crania of Chimpanzee and Gorilla present this character in a slight degree, it is never so marked in them as in *Simia*.

(c) The crowns of the molar teeth are crenated, and consequently the cusps are obscured.

(d) The mandible is, relatively to the rest of the skull, of large dimensions.

III. *Anthropopithecus* (Chimpanzee).

Distinguished by its absolute size from the skull of *Hylobates*.

Distinctions from *Simia* are as indicated in Section II.

(a) The supra-orbital ridges are continuous across the forehead.

(b) The nasal bones though flat and short are laminar and not splint-like.

(c) The crowns of the molar teeth bear distinct, but not very large cusps.

(d) The mandible is relatively smaller.

The following are the distinctions between the crania of Chimpanzee and Gorilla.

(a') The skull of the Chimpanzee is smaller, the cranial part is relatively larger, and not characterized by such large ridges as the skull of Gorilla.

(b') The nasal bones are shorter (not extending far below the level of the inferior orbital margins), and their outer margins are more nearly parallel to one another than in Gorilla.

(c') The nasal aperture tends to be pyriform in contour.

(d') The molar teeth are much smaller and bear less prominent crowns. But the incisor teeth are sometimes larger than those of the adult Gorilla, though all the other teeth are smaller than in that animal.

IV. Gorilla.

The skull is distinguished by its actual size from that of *Hylobates*.

The following are the features distinguishing the skull of the Gorilla from that of the Orang-utan.

(a) As in *Anthropopithecus*, the supra-orbital ridges are continuous across the forehead.

(b) The nasal bones are splayed and wide, though flat. The face is less markedly depressed, and is described as *katantognathic*, as opposed to the *simognathic* form encountered in the Orang-utan.

(c) The molar teeth bear large cusps.

(d) The cranial ridges are very large.

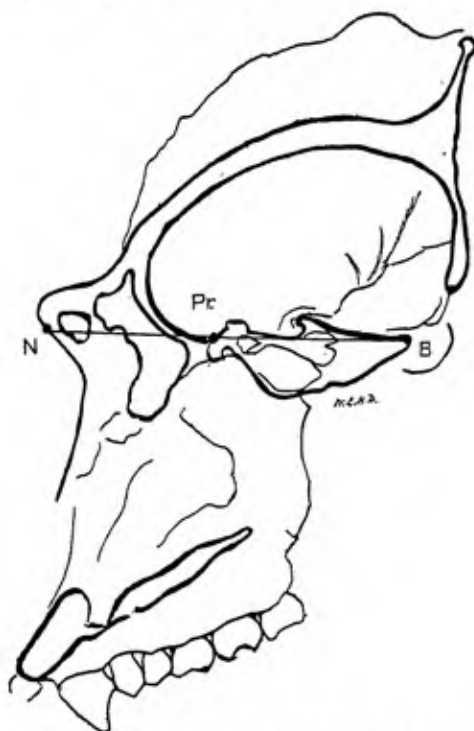


Fig. 148. Mesial section of the skull of an adult male Gorilla ($\frac{1}{2}$ nat. size).
(From a specimen in the Liverpool Museum.)

And the features which differentiate the skulls of the Gorilla and the Chimpanzee are as follows :

(a) The whole skull of the Gorilla is larger: the facial part is relatively larger: the cranial ridges are very large and prominent.

(b) The nasal bones are long; at their inferior margins they expand widely and end at a level well below that of the inferior orbital margins.

(c) The nasal aperture is ovate rather than pyriform.

(d) The molar teeth bear very large cusps and are larger than in the Chimpanzee.

From external features we pass to those revealed when the skull is sectionized in the median sagittal plane, and the examination of such sections is to be particularly recommended as leading to important conclusions on the essential differences between the skulls of Simiidae and Hominidae. The conditions presented by skulls of adult specimens will be considered first.

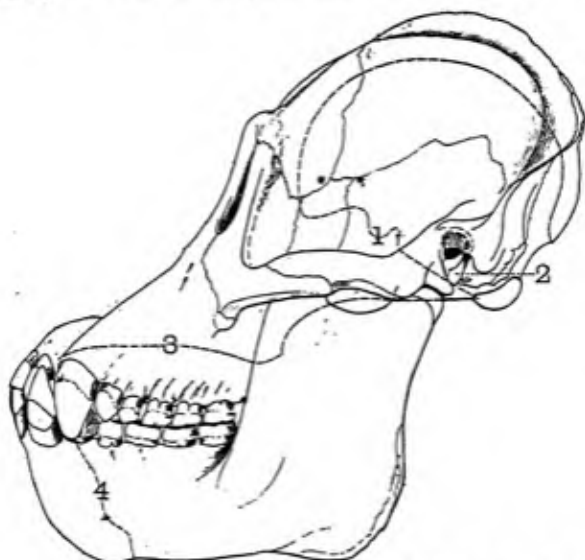


Fig. 149. Skull of an adult male Orang-utan ($\frac{1}{2}$ nat. size). (From a specimen in the Cambridge Anatomical Museum.) The interior of the skull and other points in the median plane are shown in projection by interrupted lines. The references to numbers are as follows:—

1. Sella turcica.
2. Tympanic bone.
3. Level of hard palate.
4. Deep surface of mandible.

If we examine the skull of an adult male Gorilla thus prepared (Fig. 148) the relative development of the facial components is as distinct as when the exterior of the skull is observed. The skull of an Orang-utan presents analogous features, as may be seen in Fig. 149. Comparisons with the human skull may be instituted conveniently by reference to the next illustration (Fig. 150). Here the specimens are arranged from right to left in a sequence which may be termed an "ascending" one. Continuing the inspection of the facial portion of the skull, attention is directed to the points

following. The characteristic prognathism of the ape is very marked. The constituent elements of the nasal septum correspond individually to those seen in a similar section of a human skull, the differences consisting in the details of contour and conformation. In relation with the greater size of the maxilla the system of air-spaces is more extensive in the simian skull; this is best seen when the nasal septum is removed (or when that side of the skull which does not include the septum is examined). The air-spaces are produced by an "invading" tissue, to wit the mucous membrane lining the nasal fossae. The extraordinary power of absorbing osseous tissue possessed by the cells of this tissue is not

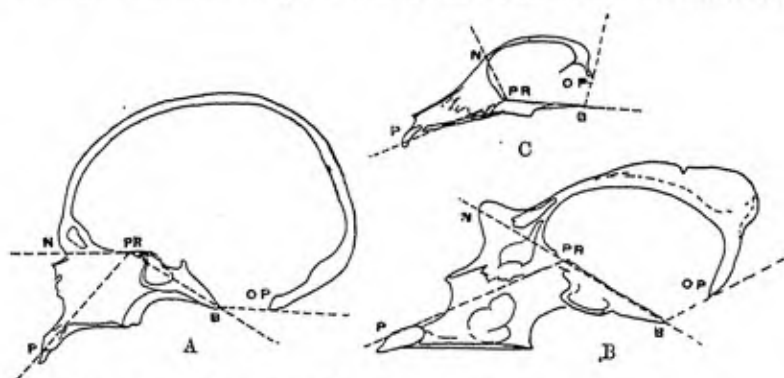


Fig. 150. The sphenothymoidal, sphenomaxillary, and foraminobasal angles are shown in the crania of (A) a New Britain native (male); (B) a Gorilla (male); (C) a Dog. N, PR, B, Sphenothymoidal angle; P, PR, B, sphenomaxillary angle; PR, B, OP, foraminobasal angle.

devoid of significance, when their origin from ectodermal cells is recalled to mind. However produced, the air-spaces confer an obvious advantage, viz. that the weight of the skull is reduced without sacrifice of strength, and also without loss of surface for the attachment of muscle-fibres.

The ape is seen to possess extensive sinuses in the sphenoid, ethmoid and maxillary bones, but not always in the frontal bone, a point wherein the Orang-utan differs from the African Simiidae (Chimpanzee and Gorilla), which are here more closely allied to man than is the first-named form. If the maxillary antrum in the skull of a Gorilla be exposed on the facial aspect of the jaw, a large bullous dilatation of the nasal duct will be

seen projecting into the maxillary antrum, along the roof of which the infra-orbital nerve runs in a bony canal. In the Orang-utan, the part of the frontal bone, which is excavated by the air-sinuses in the other apes, is a solid mass which may attain a thickness of nearly 20 mm.: seen in section, this thickness is reduced to about a quarter of that amount at the coronal suture, and the latter dimension is retained to the region of the lambdoid suture, where it is increased by the ridge which crosses the skull in a position corresponding to the lambdoid suture in man.

In contrast to the human skull, the bones of the cranial vault thus form an arch of much less bold proportions, and this is perhaps most noticeable at the occipital end of the skull, which gives the impression of having been arrested in development, leaving the occipital arc but slightly curved, and the foramen magnum consequently midway between the posterior and the inferior aspects of the skull. Again, the greatest longitudinal diameter measured from the glabellar point on the brow-ridges (or between them), passes to the external occipital protuberance in the crania of most apes¹. The skull of the Orang-utan (cf. Fig. 149) may provide a second point equidistant from the brow, but below the external occipital protuberance. In the vast majority of human crania, the diameter of greatest length ends posteriorly at a point *above* the external occipital protuberance. The exceptions include certain prehistoric crania, notably that from the Neanderthal. The latter is "simian" in this respect.

On the endocranial surface, only faint impressions mark the former positions of the cerebral convolutions². Grooves for the lateral sinuses (of the dura mater) diverge symmetrically from the torcular in the mesial plane, and are of equal size, the lack of symmetry (usually due to the preponderance of the sinus on the right side, and associated with right-handedness) found in human crania being absent here. The superior petrosal sinus may be almost completely roofed-in by bone, a bony bridge may be formed over the Gasserian ganglion, and the anterior clinoid process may

¹ Cf. Schwalbe 1901. *Bonner Jahrbücher*; also *Verhandlungen der deutschen anatomischen Gesellschaft in Anat. Anz.* 1901. *Versammlung, Bonn.*

² Cf. Schwalbe's description of the disposition of the endocranial impressions (*Zeitschrift für Morphologie und Anthropologie*, Band VII. 1904).

be connected by an osseous bar with the posterior process of that name. (The invasion of the floor or base of the anterior fossa by the frontal bone may be recalled here as distinguishing the African Simiidae from the Orang-utan and from Man.) The orbital roof is much steeper than in Man for it is still comparatively free from the displacement due to an actively-growing brain. The basis cranii includes the ethmoid, sphenoid, and occipital elements, but a crista galli does not exist in the Simiidae as a rule, and is absent from the specimens shewn in the illustrations. Anteriorly, the nasal spine of the frontal bone will be seen to be rudimentary, and in the Orang-utan the superior maxilla may come into the section in place of the nasal bone, as a consequence of the diminutive size, or extent, or of the absence of the latter element. But it is to the arrangement of the ethmoid, sphenoid and basi-occipital elements of the cranial base that special attention must be given.

It will be seen (cf. Figs. 149 and 150 B) that anteriorly the line of section of the upper margin of the ethmoid forms a plateau, nearly horizontal in direction, and that passing backwards from this, the line of the upper margin of the sphenoid is (with the exception of a hillock representing the section of that portion of the presphenoid which lies between the two orbito-sphenoids) practically continuous with the clivus, the line passing almost directly to the margin of the foramen magnum without interruption. The point to which attention is drawn is that this line forms with that of the upper margin of the ethmoid an angle salient endocranially, open below, and moreover widely open, approximating to the value of 180° , or two right angles. A glance at the human skull (cf. Fig. 150 A) shews the inclination of the two lines to be represented by a very much smaller angle. There are various ways of measuring this angle, and these will be described in detail in another connection, but for the moment it will suffice to call attention to the general appearance. The conclusion is, that in the simian skull the basal elements are arranged nearly in line, but that in the human skull this line is inflected; this inflection constitutes an important peculiarity of the human skull.

If we pass beyond the limits of this group of animals and turn our attention first to the lower Primates, and secondly to other mammals, we shall find that the straightness of the series

of basal elements becomes more marked as we descend the series, and that long before we leave the Primates the straightness is interrupted, and that in the following way.

If we suppose the central part of the series of bones, viz. the sphenoid and the basi-occipital (B. Pr., Fig. 150), to be the more fixed portion of the base, then we can describe the condition obtaining in the human skull as one in which the ethmoidal element (Pr. N., Fig. 150) is bent, or inflected, strongly downwards from the anterior end of this fixed portion. And proceeding to the simian skull, the appearance is such that the ethmoidal element is bent downwards to a smaller degree, so much less in fact that it is almost in line with the fixed portion as just defined. Lastly, when we examine the skull of a lowlier primate form such as *Mycetes* (Cebidae), the condition is such that the ethmoidal line is so to speak reflected, or bent, not downwards, but upwards (as in the Carnivora; cf. Figs. 150 c and 152) with regard to the more fixed element.

We may now turn our attention to the region of the foramen magnum. This is placed in the simian skull rather at the junction of the posterior and inferior aspects of the cranium, than frankly on the inferior aspect as in Man.

A line (Op. B., Fig. 151) drawn from the anterior to the posterior median point on the margin of this foramen represents what is described as the "plane of the foramen magnum" (Cleland called it the "posterior base of the skull" but the former name may be retained for the moment); the line representing this plane (and therefore the plane itself), will be found to be inclined to the spheno-basilar or "fixed" portion of the base (B. Pr., Fig. 151), in such a way that the angle between the two is salient downwards (cf. Figs. 150 A and 151): moreover in the Simiidae

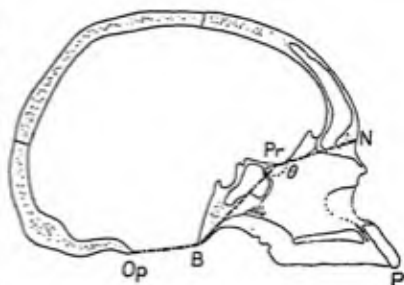


Fig. 151. Cranium of an aboriginal native of Australia (Hominidae) bisected in the median sagittal plane. N. Pr. represents the anterior or ethmoidal portion of the cranial base; Pr. B. is the middle or basi-occipito-sphenoidal portion; B. Op. represents the plane of the foramen magnum.

the angle is a large one (varying from about 120° to 140°). Turning to the human skull, we find that the mean value is rather greater (the variations ranging from about 137° to 157°). But if now we turn again to the lower Anthropeoidea, to the lowlier primate forms and mammalian orders, we find that the angle is very much smaller, and has much more nearly the value of a right

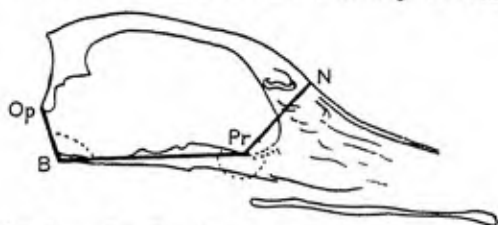


Fig. 152. Cranium of a Dog (*Carnivora*, *Canidae*) bisected in the median sagittal plane; to show the two sections into which the cranio-facial axis has been conventionally divided. The line Op. B. represents the foramen magnum; B. Pr. the "middle base," and Pr. N. the "anterior base."

angle; this is very evident in the Cynocephalous monkeys, or in *Carnivora* (cf. Figs. 150 c and 152).

We arrive thus at the conclusion that in the evolution of the form of the skull important changes have taken place in the



Fig. 153. This and the three succeeding figures represent the component parts of the cranial axis in the several stages which mark the path of evolution of the human type (Fig. 156) from the generalized mammalian type (Fig. 153, with which cf. Fig. 152). In the latter (Fig. 152) the line B. Pr. represents the comparatively stable middle portion, extending from the basion (cf. Chapter x) to the prosphenion, or most anterior point of the sphenoid bone. B. Op. represents the plane of the foramen magnum; and Pr. N., the line from the prosphenion to the nasion, represents conventionally the plane of the cribriform fossa. These indications apply to the whole series of figures (150 to 159 inclusive).

relations of the anterior and posterior basal portions respectively, to the intermediate, centrally-placed part. We see that if the latter be regarded as comparatively fixed, the anterior or ethmoidal part at one end, and the posterior or foraminal portion at the other, vary from animal to animal in such a way as to enable one to

compare them to levers fixed at each end of a bar which serves as a fulcrum to both. Further, that in the lowliest forms of the Eutherian skull the conditions may be represented diagrammatically by supposing each lever to be raised above the (more or less) horizontally placed middle portion (see Fig. 153, with which compare Fig. 152).

We have seen that in the simian skull, both levers have been depressed to a considerable extent, the anterior, ethmoidal one, more than the posterior, foraminal one; so that the diagram for the simian type of skull is as represented in Fig. 154 (with which compare Fig. 150 B):



Fig. 154.

or, since the anterior element is now the more nearly horizontal one, thus (Fig. 155):

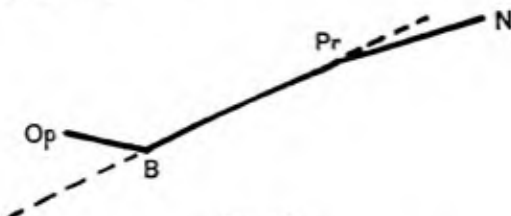


Fig. 155.

while finally, in Man, the condition incipient in the Simiidae has been brought to a further stage, and the appropriate diagram is as shewn in Fig. 156.

It is therefore to be noticed (*a*), that the human skull is characterized by the *degree* of flexion of these anterior and posterior elements upon that part of the base which lies between them; (*b*), that the simian skull indicates this change in an incipient stage, and is thus anticipatory of the human skull.

In the foregoing account an attempt has been made to give a general description only of the essential features of the cranial base, and of the changes which are seen in its evolution. No

reference has been therefore made to exact angular measurements; nor to the exact details of procedure that should be followed in drawing the lines by which such angles are included. Nor has special reference been made to the cranio-facial axis as such: this would have necessitated reference to the nasal bones with consequent complication of the description.

Such then are the chief features of interest in the sectionized skull, and their enumeration and description may be not unfitly followed by an indication of their significance. Assuming that the conformation of the cranium is largely expressive of the conformation and development of the encephalon which it encloses, it is to the latter that an appeal must be made in elucidating the

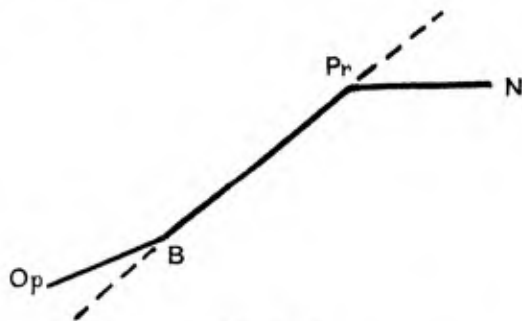


Fig. 156.

differences in the several crania investigated. Nor will the appeal be made in vain. For in the lowly Mammal and lowly Primate, the encephalon is still, in the great majority of cases, relatively small, and the cerebral hemispheres have not assumed the exuberance of growth which is a characteristic of the higher forms. When this tendency to cerebral growth has been initiated, it is found on the inferior aspect of the cerebrum that the base of the brain, the floor of the third ventricle and the allied and adjacent structures remain comparatively passive, while the cerebral hemispheres tend to expand in all directions, anteriorly, posteriorly, and laterally, upwards and downwards.

A glance at the series of diagrams of the sections of skulls will shew how such expansion implies pressure in those directions; acting anteriorly, this will force the cribriform fossa first forwards

and ultimately downwards, the transition being capable of representation by the movement of the anterior lever of our diagram (Pr. N., Fig. 153), the active force being indeed the intrinsic cerebral growth. Posteriorly, similar expansion drives backwards and then downwards the occipital wall of the cranium, and with it the foramen magnum in a similar way, capable too of similar representation (see Figs. 150 to 156 incl., pp. 225 and 231).

Expansion upwards produces the bold vaulting of the cranial arc, and in all these respects it is to the human cranium that we are led by the successive stages assumed in the lower and higher quadrupedal monkeys respectively, and then in the Simiidae themselves. In Man the effect is at a maximum, the lower Primates merely suggesting the trend of development.

But at this juncture, warning must be given of a remarkable secondary change experienced by the hinder parts of the cranial envelope. It is shewn by the position, or more properly the angle of inclination of the foramen magnum. It comes to light when we enquire how the infantile skull compares with that of the adult, and whether the individual recapitulates in his person the ancestral stages of his kind.

As a matter of fact, when averages are taken, it is found that in children of less than five years of age the typical "human" mode of conformation is more marked than in the adult¹. In order to make the point clear, we must reconsider once more the inclination of the various segments of the cranial base to one another. The accompanying figure (Fig. 157) shews the positions of the foramen magnum (in relation to the line B. Pr.) in a lowly mammal, in the young child, and in the mature human being respectively. Clearly the latter is tending to regress towards a lower condition as compared with the child. The process leading to the production of the typical human conformation seems to be actually reversed after childhood has been left behind.

This secondary process or reversal may be compared to the action of "focussing-up" with the fine adjustment of a microscope. It was discussed several years ago by Professor Manouvrier.

¹ Bolk, *Koninklijke Akademie van Wetenschappen*. Dec. 24, 1909.

More recently three investigators¹ have published the results of their studies on this and allied points, and they have confirmed and extended the work of Professor Manouvrier.

In the case of the human skull, this process of "correction" is not nearly so evident as in those of some other animals, yet its existence is undeniable. In the early stages, brain-growth proceeds with so much momentum that it oversteps the mark. Then the momentum is gradually lost, thus favouring the action of other agencies which make their appearance and become effective.

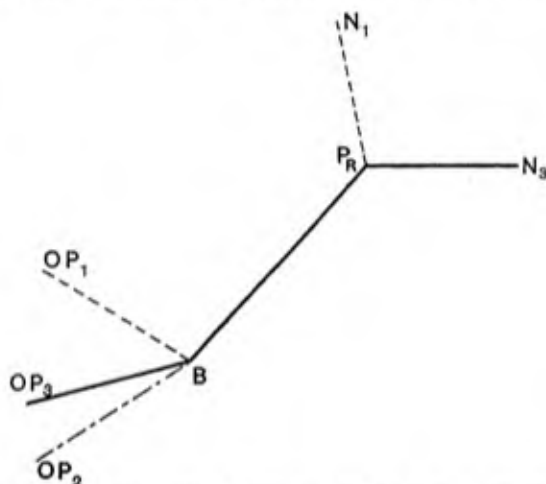


Fig. 157. Diagram illustrating differences in the inclination of the foramen magnum (Op. B.) to the middle portion (B. Pn.) of the cranial base. (Cf. Figs. 150 to 156 incl.)

OP ₁ . B.—B. Pn.	is the angle of inclination in the Dog.	(Cf. Fig. 150.)
OP ₂ . B.—B. Pn.	" " "	Child.
OP ₃ . B.—B. Pn.	" " "	Adult Man.

These effects are very striking in the skulls of young and of old Gorillas, which have been studied by Professors Bolk and Keith (*op. cit.*). Again, the South American Howling Monkey (*Mycetes*) is distinguished because the reversal goes to an extreme in this instance (Leche²). On the other hand it is suggested that the process is non-existent in the small *Chrysothrix* monkey (also a

¹ Bolk, *Koninklijke Akademie van Wetenschappen*. Nov. 27, 1909; Dec. 24, 1909. Keith, *J.A.P.*, Vol. XLIV. Part 3, April 1910. Leche, *Zoologisches Jahrbuch*, Supplement xv, 2 Band, 1912.

² Leche, *op. cit.*

South American form). If this be so, *Chrysothrix* is distinguished in this way not only from the other Primates, but from a large number of other mammals.

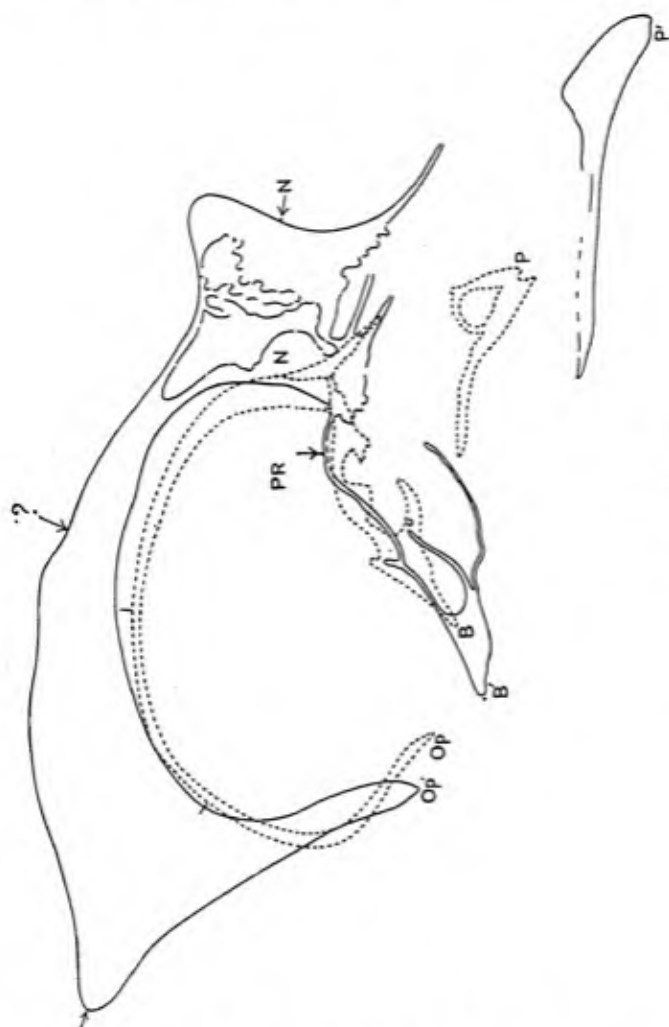


Fig. 158 ($\times 4$).

But the question now arises, How is such a reversal of the relative position and inclination of the foramen magnum brought about? In reply to this enquiry, attention is directed to three

points. Two of these can be understood best by reference to the accompanying illustration (Fig. 158) in which a tracing (punctuate line) from a young Gorilla skull is superimposed upon a similar tracing (continuous line) from an adult individual.

1. The basal plate B. PR. elongates with age, and the point B. is brought backwards till in the adult it occupies a new position (B'). This change alone is sufficient to alter the inclination of the plane of the foramen magnum (Op. B.) as shewn in the change produced in the angle Op. B. PR.

2. The next illustration (Fig. 159) is taken from crania of young and adult examples of the Orang-utan. Here the basal

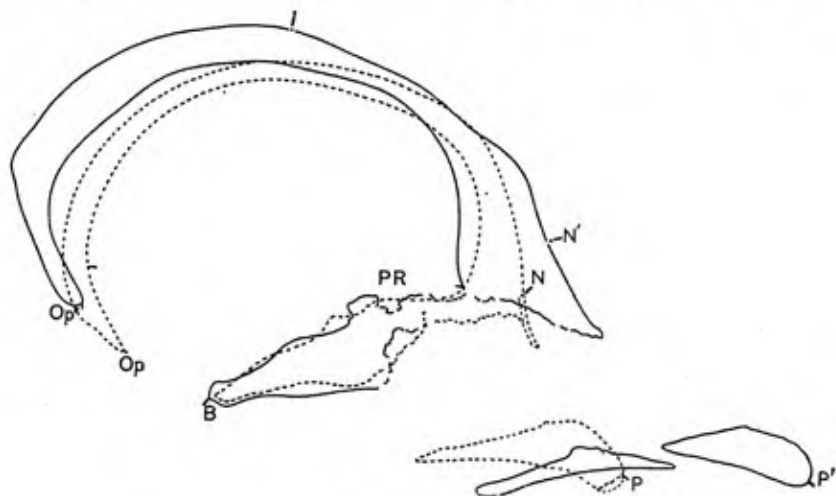


Fig. 159 ($\times \frac{1}{2}$).

plate of the young individual (punctuate line) has attained its full length. But the hind part of the skull has still to undergo a change in position. This change is partly independent of and accessory to the elongation of the parts between Pr. and B.; it results in the displacement of the point Op. backwards to a new position (Op'). This second change is undoubtedly related to the development of the face, i.e. of the jaws and teeth. The amount of this development may be gauged by comparing (in Figs. 158 and 159) the facial parts of the skulls concerned, especially in regard to the foremost point (P.) of the upper jaw.

To support the enlarged head with its increased weight, the muscles at the back of the neck hypertrophy and extend their areas of attachment about the occipital region. The inion (or point of attachment of the ligamentum nuchae (L.) moves upwards, the whole of the cranial arc or vault is elongated and slightly depressed, and the final result on the foramen magnum is that indicated by the position of the point (Op').

3. The last factor to be noticed is an increased growth of the cerebellum. In order to explain this change in an adequate fashion, a much more detailed exposition is needed than can be provided here. Suffice it to say that if the cerebellum becomes enlarged in an antero-posterior direction, it will tend to thrust backwards the lower part of the occipital bone (between I. and Op., Figs. 158 and 159) and will thus cooperate with the factors described above (as 1 and 2 respectively) in securing the final result.

In concluding this sketch of a very complicated process, I must add a few remarks by way of comment.

(a) For the accurate comparison of the various skulls, a first requisite is the employment of a reliable "base-line" to which the successive tracings can be fitted. This need has been realized by the three authorities cited above. And it is remarkable that Professors Bolk and Keith, who have studied principally the skulls of the large anthropoid apes, employ lines which are nearly identical, representing closely the longer diameter of the brain, or to be precise the longest diameter of the cranial cavity. Professor Leche differs in selecting the line of the palate (posteriorly to the anterior palatine foramen); but it is to be remarked that this is very closely *parallel* to the base-lines adopted by his colleagues, though I am not aware that this coincidence has been recognized.

(b) The parts of the skull beneath the frontal lobes of the brain undergo comparatively few secondary changes in the later (post-natal) period. Yet I believe that the enormous extension of air-spaces in the brow-ridges of the Gorilla must have an effect in the case of that animal, though the Orang-utan may not be affected thus. Such changes would be supplementary to and in the same direction as those already described.

(c) Professors Bolk and Keith note that the brain (or the cranial cavity) of the Gorilla is not increased in sectional area after a very early stage in infancy. Indeed, actual diminution of the vaulting is described, and is demonstrable. I find it hard to believe that the arrest or diminution is absolute, and I have evidence to shew that while the height of the cranium is decreased, some compensation takes place by way of an increase in transverse width. This is naturally inappreciable when longitudinal sections are

studied, and I should be prepared to find my suggestion confirmed when a correspondingly detailed study of coronal or horizontal sections has been undertaken. At present, however, the amount of information on this point is comparatively scanty.

(d) Reference has been made to the influence of the nuchal muscles on the form of the cranial envelope. This aspect of the question has been studied by Professor Leche in greater detail than by the other observers. A very important point is involved, viz. how far the muscles are capable of influencing the cranial form. The authorities are divided on this question. I have formed the opinion that Professor Leche is right in ascribing an important part to the nuchal muscles, though (as I understand his account) he demurs to the view whereby an equally potent force is granted to the temporal muscles. In this place it must suffice to indicate the diversity of views, and to repeat that the changes under discussion are encountered in many mammals, and that the factors are numerous and variable in intensity. All this is admirably stated by Professor Leche.

(e) Mention has been made [cf. paragraph (b) *supra*] of the frontal sinuses and the jaws. An account of the development of these would need a separate section. The subject is important here on account of its intimate relation to the processes of cranial development, i.e. the evolution of the brain-case proper. Again with advantage reference may be made to the publication of Professor Leche. The changes attain in some ways a maximum of intensity in the animal form (*Myeetes*) studied by him; and the Howling Monkey is therefore of much use in enabling us to recognize the slighter degrees of change met with in other animals. In this part of the subject, the question of the air-spaces in the facial bones needs even further study than has been accorded to it by Professors Bolk and Keith; and in particular, the remarkable extension of air-spaces into the palatine roof of the Chimpanzee (as recorded by Professor Bolk) should be specially noted.

(f) A word of warning remains to be given in regard to the "fixity" of the central part of the cranial base. This part is included between the points B. and Pr. in the various illustrations (viz. Figs. 150 *et seq.*). The fixity or constancy of this part (B. Pr.) is not absolute, for even this central portion participates in the changes consequent on the increased size of the brain. For this reason, this line is not entirely satisfactory as a "base-line," and although it was employed in that way by Huxley, we have seen [paragraph (a) *supra*] that it has been superseded by other lines in recent investigations. Yet for the general realization of the processes attendant on the evolution of the skull in Man and the Simiidae, this line still possesses advantages so great and the lack of fixity is relatively so small that I decided to retain it in the first instance.

From the foregoing paragraphs we may learn how the study of the skull in various types of animal (whether mammals or other) gives guidance as to their cerebral or encephalic con-

formation. Hence the study of the osteology of existing animal forms becomes paramount in importance with respect to the study of extinct types which we can know only through their skeletal remains. Finally we learn from the minute study of the skulls of the large anthropoid apes that they are evidently highly-specialized examples of Primate mammals. The same conclusion will be drawn from the other anatomical systems of these animals, and features are not lacking to shew that in some respects the Simiidae surpass even the Hominidae in point of structural (morphological) specialization. Returning to the skull (as the special object of study in this chapter) a table can be drawn up to illustrate some details of this simian specialization more clearly. Such a table (and no pretence is made that this is exhaustive) should be regarded as much more than a mere list of contrasts. For upon the results of an examination of a balance-sheet of this kind, anatomists will form an opinion as to the relations of the two forms compared therein. In the present instance, we must conclude that the existing anthropoid apes, constituted as they now are, did not figure in the ancestral history of Man. This conclusion is of great importance, but it does not exclude less-specialized precursors of the existing Simiidae from that distinguished ancestral position.

TABLE.

In comparison with the crania of Simiidae, the human skull will be seen to be more highly specialized and to have departed further from the generalized type in point of such features as :

- (1) Inflection of the basis cranii.
- (2) Forward position of the foramen magnum and occipital condyles (cf. Fig. 160).
- (3) Diminished dimensions of the maxilla.
- (4) Early and complete fusion of the premaxilla and maxilla.
- (5) High ascending mandibular ramus, and coronoid process with a deep sigmoid notch behind it.
- (6) Prominence of the chin.

On the other hand, the following features may be claimed

as shewing that the human skull is therein more generalized and primitive than those of the Simiidae.

- (1) Lack of bony ridges. I have to thank Mr Robson (of New College, Oxford) for pointing out that this may be a secondary acquisition.
 - (2) Large nasal bones.
 - (3) Wide spheno-maxillary fissure.
 - (4) Articulation of parietal and sphenoid bones at the pterion¹.
 - (5) Articulation of parietal and ethmoidal bones in the orbit¹.
 - (6) Uniformity in the size of the teeth.
- It should be understood, however, that these lists are not exhaustive.

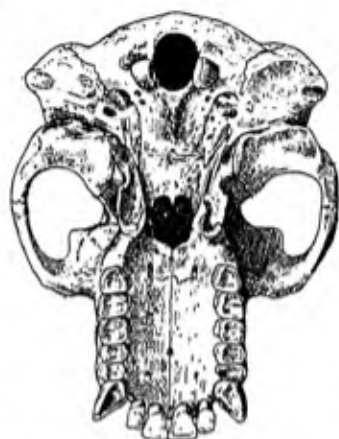


Fig. 160. Basis cranii of an Orangutan, shewing the position of the foramen magnum, far back in contrast with its position in the human skull. Fig. 150 A should also be compared with Fig. 150 B, when the same contrast will be observed. (Hose donation, Mus. Anat. Cant.)

¹ The contrast is in this instance with the African Simiidae only.

CHAPTER VI

THE DENTAL SYSTEM OF THE PRIMATES

IN enumerating the methods of investigation which have proved of assistance in elucidating the ancestral history of existing animal forms, reference was made to the study of fossil remains. From the nature of their constitution, the teeth are particularly apt to be preserved in the fossil condition, and for this reason the study of the characters of teeth claims special attention in connection with investigations undertaken with the object cited above. For the same reason it is appropriate to review, even though very briefly, the normal features of the teeth in the more representative members of the Primates, and besides the palaeontological interest of this study, another claim is presented, in view of the inferences that may be drawn from the direct morphological comparison of the several animals subjected to such an enquiry. The following notes will therefore deal in succession with the main dental characters of representatives of the Lemuridae, of the Tarsii, Cebidae, Cercopithecidae, Simiidae, and Hominidae; of these the canine and post-canine teeth will first be considered, and subsequently the characters of the incisor teeth will be briefly indicated¹, the permanent and not the transitory teeth being described first.

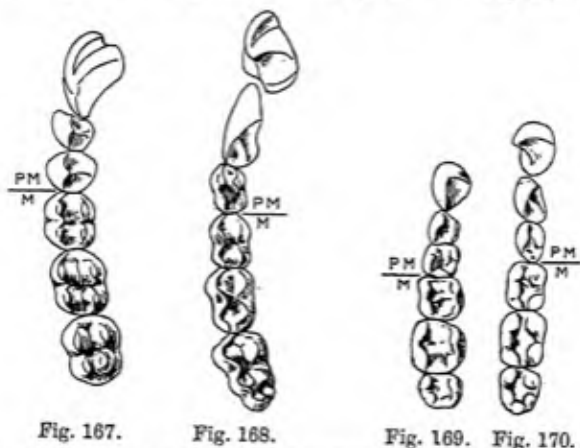
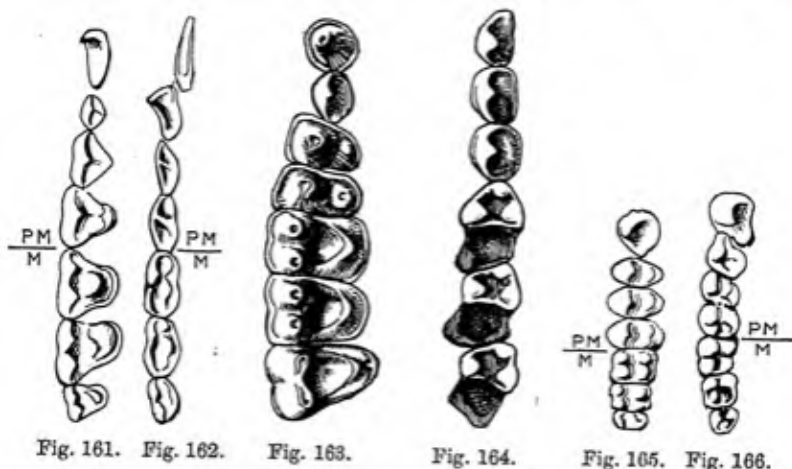
A. THE CANINE AND POST-CANINE TEETH.

LEMUROIDEA. LEMURIDAE. LEMUR VARIUS (cf. Fig. 161).

Dental formula: $i, \frac{2}{2}$; $c, \frac{1}{1}$; $pm, \frac{3}{3}$; $m, \frac{3}{3}$;

The upper teeth: Fig. 161. The canine tooth is remarkably large with a trenchant posterior margin: its socket is separated by a distinct interval

¹ The following figures (Nos. 161 to 188 inclusive, with the exception of Nos. 163, 164 and 181) represent the several teeth in their natural proportions, without reduction.



- Fig. 161. Right upper canine and post-canine teeth of a Lemur. (No. 4, Mus. Zool. Cant.)
- Fig. 162. Left lower canine and post-canine teeth of a Lemur. (No. 4, Mus. Zool. Cant.)
- Fig. 163. Right upper canine and post-canine teeth of *Tarsius*, $\times 4$. (From a specimen in the Cambridge Museum and partly after Hubrecht.)
- Fig. 164. Left lower post-canine teeth of *Tarsius*, $\times 4$. (Mus. Anat. Cant.) The lower canines are shewn in Figs. 58 and 181.
- Fig. 165. Right upper canine and post-canine teeth of *Cebus capucinus*. (No. 1093, Mus. Zool. Cant.)
- Fig. 166. Left lower canine and post-canine teeth of *Cebus capucinus*. (No. 1093, Mus. Zool. Cant.)
- Fig. 167. Right upper canine and post-canine teeth of a *Macacus* monkey. (Cercopithecidae.)
- Fig. 168. Left lower canine and post-canine teeth of a *Macacus* monkey. (Cercopithecidae.)
- Fig. 169. Right upper canine and post-canine teeth of *Hylobates mülleri*. (W. L. H. D. priv. coll.)
- Fig. 170. Left lower canine and post-canine teeth of *Hylobates mülleri*. (W. L. H. D. priv. coll.)

(diastema) from the lateral incisor in front of it, and from the premolar behind it. The premolar teeth are three in number, and increase in size from before backwards; the first is very small with a relatively immense, sharp, central cusp, supplemented by minute anterior and posterior cusps. The second premolar tooth is larger, the central cusp still immense, and an internal cusp is suggested on the surface of the cingulum (a band which surrounds the base of the tooth-crown); in the third premolar tooth this internal cusp is still more marked. The molar teeth are tricuspid (or tritubercular, cf. p. 283) and the cingulum is distinct, forming internally a prominent band which skirts the inner of the three cusps; the other two cusps are external (cf. Fig. 161). The third and last molar tooth is much smaller than the second, and as this is usually smaller than the first, the series diminishes backwards. In the mandible (Fig. 162) the formula (*v. supra*) requires some elucidation, for the canine tooth (judged by the formula) is apparently incisor-like in form, and it is also procumbent, or directed horizontally forwards like the definite incisor teeth. Moreover, the first premolar tooth resembles a canine tooth. The question of the identification of these teeth is still in doubt; Forsyth-Major (*Geological Magazine*, 1900) has adopted the view which regards the canine-like tooth as the genuine canine, and the outer incisor-like tooth as an incisor, thus providing the mandible with a dental formula $i, 3; c, 1; pm, 2; m, 3$; different, that is, from the maxillary formula $i, 2; c, 1; pm, 3; m, 3$. But it is to be noticed that against this view may be urged the fact that the canine-like premolar tooth although admittedly canine in form, yet closes (in the bite) posteriorly, and not anteriorly, to the upper undoubted canine tooth. Yet this posterior position of a lower canine tooth is a phenomenon of extreme rarity, and though Forsyth-Major defends his position by appealing to the progressive shortening of the mandible, which no doubt has occurred, still in view of the mutability of dental forms, it seems more consistent to adopt the opposite view of regarding the canine tooth of the mandible as incisiform, and the first premolar tooth as caniniform¹.

The lower teeth. All the mandibular teeth are flattened from side to side, the premolars bear one relatively immense cusp and three minute subsidiary cusps (cf. Fig. 171), and the middle premolar tooth is the smallest of the three. The molar teeth are quadricuspid, two cusps being external and larger than the two remaining and internally situated cusps, and these teeth diminish in size backwards. Such diminution backwards suggests that the jaws are undergoing a process of reduction in length which is in operation at the posterior extremity. Forsyth-Major has pointed out that, in addition to this, retraction of the mandible as a whole has occurred.



Fig. 171.
Diagram of the
first left lower
premolar tooth
of a Lemur.

¹ Flower and Lydekker, *Mammals*, p. 683, suggest that the canine tooth is absent altogether.

Nycticebus (Lemuridae). In this form (as in the Slender Loris) the molar teeth of the upper jaw are four-cusped, the cusps being arranged in two pairs, with an oblique ridge joining the antero-internal to the postero-external cusp. This arrangement is met with rarely among the Cebidae, entirely lost in the Cercopithecidae, but reappears in the Simiidae and Hominidae, where it is a marked feature.

TARSII. TARSUS SPECTRUM (Figs. 163, 164).

The dentition as a whole is decidedly primitive or archaic¹. The upper canine tooth is smaller than its lower representative, and in point of actual form, the incisors, canine and first premolar teeth do not greatly differ from each other, for all are of a simple peg-like shape. The upper molar teeth bear three cusps each ("tritubercular" type).

The lower canines exceed in size those of the upper set. Each of the lower molar teeth bears three cusps, behind which a supplementary "heel" (or "taloid") is situated (the "tuberculo-sectorial" type).

ANTHROPOIDEA. CEBIDAE. CEBUS CAPUCINUS.

Dental formula of the family: $i, \frac{2}{2}$; $c, \frac{1}{1}$; $pm, \frac{3}{3}$; $m, \frac{3}{3}$.

The upper teeth: the canine teeth (Fig. 165) are relatively enormous in size, especially in the male sex (cf. Fig. 21); the post-canine teeth present a feature of marked contrast with the corresponding teeth of the Lemuridae, inasmuch as the crowns appear much reduced in the antero-posterior direction (this is even more distinct when the lower series are compared, cf. Figs. 162 and 166). A diastema is present. The premolar teeth are three in number and bicuspid, with anterior and posterior cusps: in size they diminish progressively backwards. Of the three molar teeth, the first is the largest and the diminution in size backwards is very rapid, the last tooth being minute. The molar teeth bear four cusps, two outer and two inner, and in the species under consideration (*C. capucinus*) no connecting ridges are seen. In some forms the antero-internal and postero-external cusps may be connected by an oblique ridge (cf. Fig. 165).

The lower canine teeth correspond to the upper teeth in size, and in closing they pass anteriorly to these as in the great majority of Eutheria. The first of the three premolar teeth is pyramidal and suggests a transition from the canine form to the bicuspid premolar form: it bears one predominant cusp and a second smaller cusp, and is distinctly larger than the two remaining premolar teeth, which are bicuspid with external and internal cusps, and sub-equal in size. The three molar teeth diminish rapidly in bulk backwards, the last being clearly degenerate, and this degeneracy in the third molar tooth of the otherwise comparatively primitive Cebidae must be insisted on. Such

¹ Cf. Hubrecht, *Descent of the Primates*, 1897, p. 11. Earle, *Natural Science*, May 1897, p. 309 (with especial reference to the researches of Professor Leche).

reduction is again met with in the Simiidae and Hominidae, but must not be regarded as confined to the higher families of the Primates. The molar teeth bear three distinct cusps, two external and one antero-internal, the postero-internal cusp being quite indistinct, especially in the last tooth. The three better marked cusps are connected by rather indistinct ridges¹.

ANTHROPOIDEA. CERCOPITHECIDAE. MACACUS RHEUS.

Dental formula: $i, \frac{2}{2}$; $c, \frac{1}{1}$; $pm, \frac{2}{2}$; $m, \frac{3}{3}$. (Figs. 167 and 168.)

The canine teeth, which may in male specimens attain very great dimensions (cf. Fig. 28), are preceded in the upper jaw by a distinct diastema. The upper premolar teeth (two in number) are bicuspid but are implanted by three roots. (In the types hitherto considered, the number of roots of the premolar teeth has varied; in some teeth the root is single, and in others even in the same jaw three roots are present.) The premolar crowns shew signs of antero-posterior flattening as in *Cebus*, the outer cusp of the first tooth is much larger than the inner, and the two teeth are nearly equal in size. The upper molars bear four cusps, two external (buccal) and two internal (lingual) united in pairs by transverse ridges, and implanted by three roots. The second tooth is the largest, the first and third being nearly equal in size, though the latter may be in some instances reduced. There is no distinct indication of reduction of cusps in the third molar tooth.

The lower canine tooth corresponds in dimensions to the upper, and the first lower premolar tooth is caniniform, the lingual (internal) cusp being quite overshadowed by the hypertrophied external cusp. In all the lower post-canine teeth the roots are two in number, and the same teeth preserve the lemurine feature of lateral compression, though this is only marked in the first premolar tooth.

The three molar teeth increase in size progressively backwards: their crowns bear four cusps united in pairs by transverse ridges, and in the last tooth the posterior projection known as the "talon" is well developed and bears one or even two subsidiary cusps.

Attention is here directed to the presence of the transverse ridges upon the crowns of the molar teeth (whether upper or lower) of the Cercopithecidae, to the exclusion of an oblique ridge.

¹ The indistinctness of the postero-internal cusp is important. As will be shewn later (in Chapter XVI) the indistinctness of a particular cusp has been appealed to in support of the human characters of the fossil *Pithecanthropus erectus*. The point therein raised is that in the lower Primates, the reduction in cusps affects the postero-external (metacone) before it modifies the postero-internal cusp or hypocone (while in the Hominidae the postero-internal is the first of the two to shew signs of reduction). Herein the *Pithecanthropus* is said to agree with the Hominidae, and to differ from the Simiidae. But the incompleteness of this generalization is shewn clearly by the foregoing observation.

ANTHROPOIDEA. SIMIIDAE. *HYLOBATES MÜLLERI*: a Gibbon from Borneo.

Dental formula: $i, \frac{2}{2}$; $c, \frac{1}{1}$; $pm, \frac{2}{2}$; $m, \frac{3}{3}$. (Figs. 169 and 170.)

The upper teeth. The canine teeth are very long and slender (cf. Fig. 144) and preceded by the diastema. The premolars are bicuspid with three roots, and the first of the two is caniniform in so far as the outer cusp is much larger than the inner, the latter being very obviously a derivative of the cingulum. In the second premolar tooth such disparity is less distinct, and this tooth is rather larger than the first. The three molar teeth decrease in size successively backwards. Like the premolar teeth, they are implanted by three roots, two external and one internal, and their crowns bear four cusps, two external (lingual) and two internal (buccal) in position. It is important to note that these cusps lack the transverse connecting ridges which are so characteristic of Cercopithecidae, but which are here replaced by an oblique ridge uniting the antero-internal with the postero-external cusp. The same arrangement obtains in the Hominidae (cf. p. 289). The third molar tooth bears signs of degeneration, two posterior (lingual and labial) cusps and the oblique ridge being in some cases vestigial and indistinct.

The lower teeth (Fig. 170) situated behind the canine tooth are implanted by two roots each, these roots being anterior and posterior in position as is the general rule in the Primates. The lower and upper canine teeth correspond in development, and it is noteworthy that traces of lateral compression are perceptible in these teeth. The lower post-canine teeth still present signs of lateral compression though this feature is less conspicuous than in the Lemurs and even the Cercopithecidae; for a process of antero-posterior reduction is now being initiated, with the result of rendering the crowns of the teeth equilateral in proportions.

The first of the two premolar teeth (cf. Fig. 169) bears one very large (lingual) and a much smaller (labial) cusp; it is larger than the succeeding tooth, the crown of which is furnished with two small cusps, behind which an undoubted though minute talon is seen.

The lower molar teeth vary in different specimens, but the second tooth would seem to be the largest, next to this the first, though this and the third are in some cases equal in bulk. The crowns bear four or five cusps; viz. an anterior pair (external and internal) which may be connected by a transverse ridge¹; and a posterior pair not so connected, and between which a fifth minute cusp may be seen: the last-mentioned cusp may be regarded as representing in a reduced form the bicuspid talon, so conspicuous in the Cercopithecidae (*supra*). Finally, it should be noted that in the reduction affecting these cusps, the inner (lingual) posterior cusp is involved to a greater extent than the outer. This affects a point of controversy to which attention has already (p. 244, footnote) been drawn.

¹ This is seen in a specimen in the writer's possession.

ANTHROPOIDEA. SIMIIDAE. *SIMIA SATYRUS* (Orang-utan).

Dental formula: cf. *Hylobates*. (Figs. 172 and 173.)

In correspondence with the greater absolute bulk of these animals the teeth of the larger Simiidae are larger than any others hitherto considered. As in most of the Anthropeida, the sexual factor has an important influence upon the dentition and particularly upon the dimensions of the canine teeth. The transitory dentition is found in all the Primates so far as they are known; in the case of the higher members of this Order (cf. Figs. 145 and 147) a very close agreement with the phenomena presented by the Hominidae has been observed, and in the larger Simiidae the transitory teeth correspond in number to those found in the milk dentition of the Hominidae. The differences hitherto noticed affect the sequence in which the replacement of the transitory by the permanent teeth occurs.

To return to the teeth of the Orang-utan, we note (cf. Fig. 172) a large diastema or interval in front of the upper canine teeth: the two upper premolar teeth resemble one another more closely than in some forms previously dealt with (e.g. *Cercopithecidae*). Both are bicuspid and furnished with three roots; in both the antero-posterior diameter of the crown is diminished: in the first of the two, the outer or labial cusp surpasses in size the lingual cusp. Like the remaining post-canine teeth, the crowns of the premolar teeth are marked with fine crenations.

The crowns of the three molar teeth exhibit crenate markings in a degree which is peculiar to the Orang-utan among the Simiidae and in which it is most nearly approached by the Chimpanzee. This crenation is the expression of folding of the enamel covering the crown and is a feature of practically all developing molars in the Primates. Its persistence thus constitutes the retention of an embryonic condition. When strongly marked, and individuals present much variation in this respect, the features of the dental crown are hereby obscured. Nevertheless it is possible to make out some other points in the conformation of these teeth. The crowns are nearly equilateral and traces of four cusps are commonly seen. The first and third molar teeth are nearly equal in size and both are smaller than the second: the last tooth seldom fails to bear signs of degeneration. Of the cusps, the antero-internal and postero-external are joined by an oblique ridge similar to that seen in *Hylobates*. The postero-internal cusp shews signs of degeneration and reduction (it may be replaced by several minute eminences) before these are exhibited by the other cusps.

The lower canine tooth is long and tusk-like. The first premolar tooth is pyramidal, and the labial cusp far surpasses the lingual cusp in size. The two cusps of the second premolar tooth are subequal in size, and a suggestion of a posterior projection, or talon, is seen (as in *Hylobates*). Crenation is present as in the upper post-canine series.

The molar teeth are longer than they are wide, the last tooth being the smallest. The cusps are five in number, and the posterior intermediate cusp is often found to be much reduced in prominence in the last tooth.

In the Orang-utans supernumerary molar teeth are extraordinarily frequent, and particularly so in the male sex: the additional tooth is usually placed behind the third molar¹. This subject will be further discussed in connection with anomalies of the dentition. The great length of the roots of all the teeth has been remarked as a characteristic feature of the dentition of the

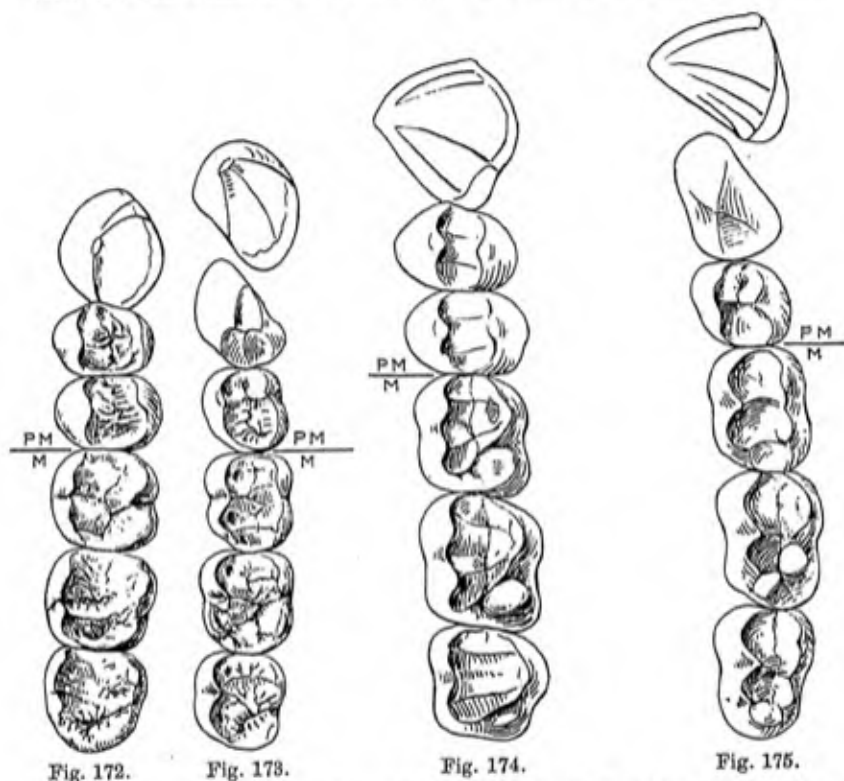


Fig. 172. Right upper canine and post-canine teeth of an Orang-utan (ad. ♂ W. L. H. D. priv. coll.).

Fig. 173. Left lower canine and post-canine teeth of an Orang-utan (ad. ♂ W. L. H. D. priv. coll.).

Fig. 174. Right upper canine and post-canine teeth of a Gorilla (ad. ♂ W. L. H. D. priv. coll.).

Fig. 175. Left lower canine and post-canine teeth of a Gorilla (ad. ♂ W. L. H. D. priv. coll.).

Orang-utan (cf. Tomes, *Dental Anatomy*, ed. 1898), while reference to Figs. 172 and 173 shews that the Orang-utan provides an excellent illustration of

¹ Cf. Bolk in *Koninklijke Akademie van Wetenschappen. Proceedings*, April 27, 1906, p. 789.

the comparatively gradual transition and transformation from one type of tooth to another.

ANTHROPOIDEA. SIMIIDAE. GORILLA SAVAGII.

Dental formula: $i, \frac{2}{2}$; $c, \frac{1}{1}$; $pm, \frac{2}{2}$; $m, \frac{3}{3}$. (Figs. 174 and 175.)

In the replacement of the deciduous (milk) teeth by those of the permanent series it is to be noticed that whereas in the Hominidae the canine teeth are replaced before the third molar tooth appears, yet in Gorilla these events occur in the reverse order. In the male Gorilla (adult) the canine teeth are enormously developed and the diastema is very evident. The upper premolar teeth bear two cusps, labial and lingual in position, but it is to be remarked that suggestions of two other cusps of minute size, situated behind these, are not uncommonly present. The labial cusps are the larger. The premolar teeth have three roots. The molar teeth are quadricuspid and the cusps stand out with peculiar distinctness: the oblique ridge joining the antero-internal and postero-external cusps is likewise unmistakable. Measurements of a number of specimens show that the last molar tooth is smaller than the first, the second being the largest of the three; so that the reduction that has been so often noticed in the third tooth is present in the dentition of Gorilla. The molar teeth are implanted by three divergent roots.

The lower premolar teeth differ not a little in appearance from one another. The first is pyramidal and bears one well-defined cusp: in the second tooth the two cusps are nearly equal in size, and behind them a small talon projects. The molars are comparatively narrow, and elongated antero-posteriorly: they commonly bear five cusps, the anterior pair of which are to some extent united, and at the same time leave the three posterior cusps isolated from one another. In some cases as many as six cusps may be seen, the posterior part of the crown bearing four of these. No confirmation appears to be given to the statement that the postero-external cusp is earlier affected by degenerated processes than the postero-internal cusp. (*v. ante*, p. 244, footnote.) While the statement (*cf.* Topinard, quoted by Fraipont, *Archives de Biologie*, vii. p. 735) as to the progressive increase backwards in the size of molar teeth does not hold good in the upper series, there is no doubt that it is true of the lower teeth¹.

ANTHROPOIDEA. SIMIIDAE. ANTHROPOTHECUS NIGER.

Dental formula: $i, \frac{2}{2}$; $c, \frac{1}{1}$; $pm, \frac{2}{2}$; $m, \frac{3}{3}$. (Figs. 176 and 177.)

As regards the canine teeth similar remarks apply to the Chimpanzee and Orang-utan. The upper premolar teeth, and indeed the whole dentition, of the Chimpanzee suggest however the human dentition much more distinctly

¹ The latter statement as well as that made in reference to the relative sizes of the molar teeth in the Orang-utan is based upon the results of measurement in adult examples. Five male Gorillas and six male Orang-utans were available.

than does that of any other Primate. Shortening of the maxillae has evidently to be recognized, and the crowns of the premolar teeth, when compared with those of Gorilla, are much reduced in the sagittal direction. These teeth bear outer and inner cusps, while as regards roots a difference may obtain, the first premolar tooth possessing three roots, the second tooth having only two.

The molars present a crown of equilateral proportions, the third tooth being degenerate both in size and in the reduction of the posterior cusps,

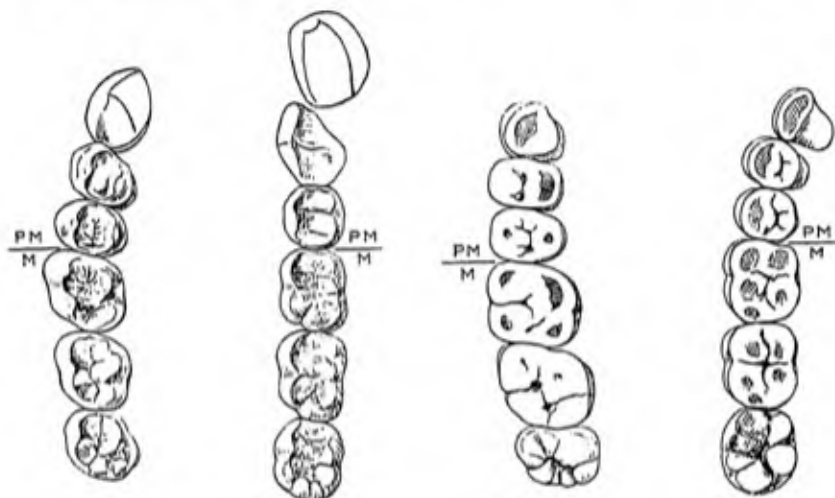


Fig. 176.

Fig. 177.

Fig. 178.

Fig. 179.

Fig. 176. Right upper canine and post-canine teeth of a Chimpanzee (ad. ♂ W. L. H. D. priv. coll.).

Fig. 177. Left lower canine and post-canine teeth of a Chimpanzee (ad. ♂ W. L. H. D. priv. coll.).

Fig. 178. Right upper canine and post-canine teeth of an aboriginal native of Australia. (Mus. Anat. Cant.)

Fig. 179. Left lower canine and post-canine teeth of an aboriginal native of Australia. (Mus. Anat. Cant.)

of which the postero-external may be more affected than the postero-internal cusp. (Thus confirmation of the statement to which reference has been made already, is provided by one of the Simiidae only.) The other molar teeth bear four cusps, viz., an anterior and a posterior pair, the characteristic oblique ridge being present as in the other Simiidae. And it is to be remarked that crenation is often distinct, though less characteristic of the Chimpanzee than of the Orang-utan. In the mandible, the premolar teeth are less like the corresponding human teeth than when the comparison is made with teeth of the upper series. For in the mandible the characters

of the premolar teeth in Chimpanzees are very similar to those of the same teeth in Gorilla, though in the Chimpanzee these teeth are distinguished chiefly by their smaller size and the persistence of crenate markings. Very similar remarks apply to the lower molar teeth, viz., that they resemble the corresponding teeth in Gorilla, but present crenate foldings of the enamel, and are less elongated in the antero-posterior direction. In comparison with the human teeth of the mandibular series, it is to be noted that the Chimpanzee does not provide the marked contrast in size between the second premolar and the first molar. The characteristic appearances are shown in Figs. 176 and 177 respectively.

ANTHROPOIDEA. HOMINIDAE. HOMO NAPIENNS.

Dental formula as in all the Catarrhine Primates: $i, \frac{2}{2}; c, \frac{1}{1}; pm, \frac{2}{2}; m, \frac{3}{3}$. (Figs. 178, 179.)

It has been already remarked that the dentition of the Chimpanzee provides in many ways a transition from the simian to the human modification of the Primate type. When the human dentition is examined in series with those of the other Primates, perhaps the most striking and peculiar feature is the reduction in size of such teeth as are situated anteriorly to the molars, viz., the premolars, canines, and incisors. This reduction is doubtless associated with the change in function determined by the greater freedom of the upper limb in man, whereby the jaws are relieved, to a larger extent than in any other Primate animal, of their prehensile function. Again, the distinctive characters of the dentition are correlated with the modifications of the cranial base to which reference has been made in the preceding chapter.

The canine teeth have almost entirely lost the predominance in size that obtains in the majority of the Primates: and the diastema is no longer present, except as an anomaly.

The upper premolar teeth are bicuspid and possess a single root, the molar teeth being furnished with three roots, which are however in the majority of the Hominidae, not divergent, but parallel, and in the third molar may be reduced to two, which may even be fused into a single peg-like root.

The molar teeth do not present crenate markings in the adult: in size, the second upper tooth is the largest, next to this the first molar tooth, while the last tooth is practically always degenerate, and may be absent. The upper molar cusps are four in number, disposed as in the Simiidae but commonly less prominent. The oblique ridge is distinct in the two foremost teeth, but often obscure, or absent from the last tooth.

In the mandible the first premolar is often nearly as large as the canine tooth, and larger than the second premolar tooth: both are bicuspid and furnished with single roots. The second lower premolar is much smaller than the first molar. At this point therefore a remarkable change in size is evident. Herein the human dentition differs from that of the three larger Simiidae (cf. Figs. 173, 175, 177, 179). The molar teeth present varying

relations in point of size: the last is often the smallest of the three; in form the crowns are less elongated in the antero-posterior direction than are the corresponding teeth in Gorilla or Anthropopithecus. The cusps are commonly four in number, and they are distinct, separated by grooves forming a crucial fissure. But in many cases, and particularly among the primitive and prognathous coloured races, a fifth cusp (the "hypoconulid" of Osborn, *Evolution of Mammalian Molar Teeth*, 1907, p. 81) is found usually on the posterior margin and between the two normal cusps.

The comparison of the length of the post-canine series of teeth has been studied by Flower (cf. the *Journal of the Anthropol. Institute*, 1885), who devised an index for comparative purposes: this dental index is based on the relation of the dental length (that is the combined lengths of the crowns of the post-canine teeth) to the length of the cranio-facial axis. (Cf. Fig. 150 B, N.)

The index is arrived at from the formula:

$$\text{Dental index} = \frac{\text{length of the premolar and molar crowns} \times 100}{\text{basal-nasal cranial length}},$$

and crania are classified according to the numerical value of that index. Thus the limits of the class divisions are at 42 and 44. Crania with dental indices of a greater numerical value than 44 are distinguished as megadont, and such crania are found to prevail in the Oceanic-negro races, while when a comparison is made with the Simiidae, these too (with the exception of Hylobates, and perhaps only in individual examples of these) are very distinctly megadont, the average value of the index far exceeding 44 and rising to 54 or more. (For other data cf. Chapter XIV.)

B. THE INCISOR TEETH.

The formula throughout the Primates is $i, \frac{2}{3}$; they are borne by the premaxilla in the upper jaw.

LEMUROIDEA. LEMURIDAE. LEMUR VARIUS. Fig. 180.

The characteristic features of the incisor teeth of the Lemuridae are as follows: (a) the upper teeth are extremely small (in some, the extinct Lemur, e.g. *Megaladapis madagascarensis*, they are vestigial or absent, cf. Standing, *Zool. Trans.*, May, 1908), and the median teeth are separated by a wide gap in the middle line of the face; (b) the lower teeth are larger and curiously styloid, they are also procumbent, that is, they are directed almost horizontally forward from the mandible and cannot therefore be of much use as incisor teeth in the ordinary acceptation of the term; (c) the apparent occurrence of three incisor teeth on each side in the mandible is explained by the view which regards the lower canine teeth as having assumed the morphological characters and the position of lower incisor teeth (it will be remembered, *v. ante*, p. 242, that the succeeding tooth, the first premolar, has to some extent replaced the normal lower canine teeth).

TARSII. TARSIVS SPECTRUM. (Fig. 181.)

The long styloid upper median incisor is supplemented laterally by a very diminutive lateral tooth; no interval separates the upper median incisor teeth (as in Lemurs). The mandibular teeth are remarkable for their number, since there are but two, one on each side. They are not (as in Lemurs) procumbent, and in their conical form, they suggest the dentition of Insectivora.

ANTHROPOIDEA. CEBIDAE. CEBUS CAPUCINUS. Fig. 182.

In the Cebidae the disparity in size between the upper and lower incisor teeth (as described in the Lemuridae) is not to be seen, but there is still a slight tendency (quite distinct in Pithecia) to procumbency in the lower incisors (cf. Fig. 21).

The median teeth are provided with chisel-shaped crowns, the lateral with conical crowns: the latter crowns when worn down by use quickly assume a



Fig. 180.

Fig. 181.

Fig. 182.

Fig. 183.

Fig. 184.

Fig. 180. Incisor teeth of a Lemur. (No. 4, Mus. Zool. Cant.)

Fig. 181. Incisor and lower canine teeth of *Tarsius spectrum*, $\times 2$. (Mus. Anat. Cant.)

Fig. 182. Incisor teeth of *Cebus capucinus*. (No. 1093, Mus. Zool. Cant.)

Fig. 183. Incisor teeth of a *Macacus* monkey.

Fig. 184. Incisor teeth of *Hylobates mulleri* (ad. σ W. L. H. D. priv. coll.)

chisel-like edge, but in the unworn condition their form is as described above. These remarks regarding the crowns of the teeth apply to the Cercopithecidae, and to *Hylobates*, *Simia*, and *Gorilla*, but not to *Anthropopithecus* or to the Hominidae.

The combined upper series is wider than the lower set. Of the upper four teeth, it is to be remarked that no median gap remains and that the outer (lateral) teeth are smaller than the median pair, while the outer angle of the crown is more open in the lateral than in the median tooth. Of the lower teeth the lateral surpass the median pair in size.

ANTHROPOIDEA. CERCOPITHECIDAE. CERCOPITHECUS. Fig. 183.

The lower incisor teeth are still less procumbent in the Cercopithecidae (cf. Fig. 28); the upper median incisors, as in all the Anthropoidea, are in contact and the upper median teeth much surpass the lateral teeth in size. The median and lateral lower incisor teeth are nearly equal in bulk, the lateral pair being rather stouter than the median.

ANTHROPOIDEA. SIMIIDAE. *HYLOBATES* (mülleri). Fig. 184.

The incisor teeth have the general characters of those of Cercopithecidae. It is to be noticed as a difference (cf. Fig. 183 with Fig. 184) that in *Hylobates* the crown is much less extensive in the vertical direction, both absolutely and relatively. The comparative smallness of the crown is seen again in the Orang-utan.

ANTHROPOIDEA. SIMIIDAE. *SIMIA SATYRUS* (Orang-utan). Fig. 185.

The median upper incisors far surpass the lateral incisor teeth in size: the small size of the upper crowns is very remarkable. Of the lower teeth the median pair exceed the lateral pair in bulk usually but not always.

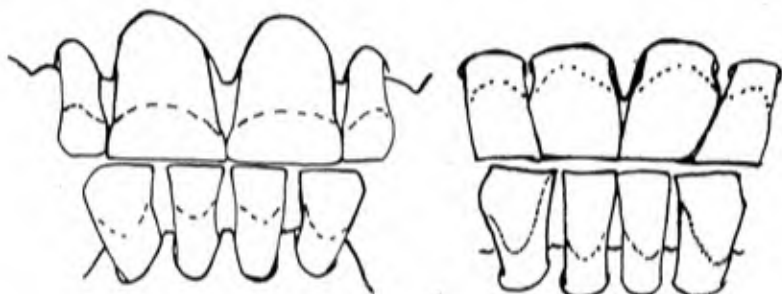


Fig. 185.

Fig. 186.

Fig. 185. Incisor teeth of an Orang-utan (ad. ♂ W. L. H. D. priv. coll.).

Fig. 186. Incisor teeth of a Gorilla (ad. ♂ W. L. H. D. priv. coll.).

ANTHROPOIDEA. SIMIIDAE. *GORILLA SAVAGII*. Fig. 186.

The difference in the sizes of the median and lateral upper incisor teeth is less marked in the Gorilla, but the median pair are still the larger. In the lower series the opposite proportion obtains. The upper crowns are more extensive than in *Hylobates* and *Simia*, and recall the type found in Cercopithecidae.

ANTHROPOIDEA. SIMIIDAE. *ANTHROPOPITHECUS NIGER*. Fig. 187.

The upper median teeth are larger than the upper lateral teeth; the crowns are extensive (as in Gorilla); of the lower teeth, the median and lateral pair are nearly equal in bulk. It is very noteworthy that in the Chimpanzees, the incisor teeth may often equal or even surpass in bulk the incisor teeth of the male Gorilla, while the molar teeth and indeed the whole skull of the Chimpanzee are much smaller than that of the male Gorilla.

ANTHROPOIDEA. HOMINIDAE. HOMO SAPIENS.

An aboriginal native of Australia (Fig. 188). The upper median incisors are but slightly larger than the lateral incisors; the crowns are extensive; of the lower teeth, the lateral pair slightly exceed the median pair in bulk.

The milk, temporary or deciduous dentition of the Primates comprises a smaller number of teeth than that found in the permanent set. Among the Anthropeida, the Platyrrhine and Katarrhine groups are moreover distinguished by the deciduous dentition as clearly as by the later teeth. Thus in all the Anthropeida the deciduous dentition includes two incisors and a canine tooth on each side of the jaws, and in the upper and lower jaws alike. To these teeth, three deciduous teeth ("milk-molars") are to be added in the Platyrrhine division, and they are subsequently replaced by the three distinctive premolars of those animals. The Katarrhine division has but two deciduous molars, i.e. the number here corresponds to that of the permanent teeth which replace them later. The following formulae are employed by

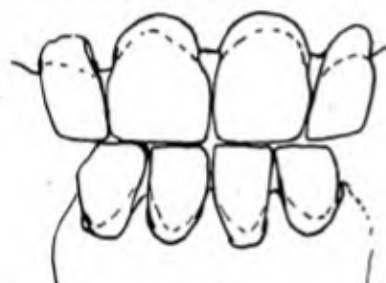


Fig. 187.

Fig. 187. Incisor teeth of a Chimpanzee (young ? W. L. H. D. priv. coll.).



Fig. 188.

Fig. 188. Incisor teeth of an aboriginal native of Australia. (Mus. Anat. Cant.)

Professor Bolk¹ for comparing the numbers and the characters of the deciduous and permanent dentitions. The permanent teeth are here distinguished by capital letters: the formulae are accordingly:

Katarrhinae	2 I 1 C	2 P	
	2 i 1 c	2 m 3 M	upper jaw.
	2 i 1 c	2 m 3 M	lower jaw.
	2 I 1 C	2 P	
Platyrrhinae ²	2 I 1 C	2 P	
	2 i 1 c	3 m 3 M	upper jaw.
	2 i 1 c	3 m 3 M	lower jaw.
	2 I 1 C	3 P	

¹ Koninklijke Akademie van Wetenschappen, 1906, Ap. 26, p. 782.

² For the Hapalidae (Marmosets) the Platyrrhine formula must be changed by substituting two permanent molars above and below $\left(\frac{2M}{2M}\right)$ for the three teeth indicated here.

In all cases the permanent dentition is initiated by the appearance of the first (permanent) molar. This tooth does not replace a deciduous tooth but it emerges behind the most posterior element in that series. The third molar tooth is the latest to emerge in the completion of the permanent dentition in Man, but in the Gorilla the canine teeth may be delayed after the emergence of the third molars. Beyond this, little or no information is available concerning the mode of replacement of the deciduous teeth in the Primates other than the Hominidae. In the latter, the deciduous teeth are functional from the second to the sixth year (approximately). This is a long period in comparison with some other mammals. Leche has recently pointed out (in an admirable memoir, *Zool. Jahrbücher*, Bd. xxviii. Heft 4, 1909, p. 451) that the functional period varies greatly in duration even within a single Order. Thus the Badger is distinguished by the extremely short duration of this period when compared with the Cat. The point is not without importance for Leche is able to point to at least one character of the deciduous teeth (*viz.* the absolute dimensions) which is related to the length of the functional period.

Apart from all this, the deciduous dentition is of importance in connection with problems of phylogeny, since some authorities (*e.g.* Leche) hold that the deciduous teeth present characters which at an earlier period were borne by ancestral relatives. This point will demand further consideration in the sequel.

The numbers and the general characters of the teeth having been reviewed, enquiry is now to be made into the evolution of the teeth in the Primates. This will be approached from several directions, and the following departments of research and study call for separate treatment:

- I. Variations of the teeth in the direction of increase in the number.
- II. Variations in form.
- III. Variations in position.
- IV. Variations in the direction of reduction in the number of teeth.
- V. Evolution of different dental types such as the incisors, premolars, etc.
- VI. Theories of cusp development and the origin and fate of cusps.

I. Variations by way of increased numbers.

Under this head, the teeth of the permanent series will be mainly considered. Retention of the deciduous teeth will naturally provide an apparently increased permanent dentition. Thus Guttman (quoted by Kükenthal, *Jahresbericht der Anatomie*, 1901), records the case of a youth (aet. 19) in whom nearly all the deciduous teeth were retained in the presence of their successors. Such examples are not relevant here, though one exception to the exclusion of "retained milk-teeth" must be made. This is the case of persistence of the second deciduous or "milk" molar tooth. But inasmuch as the tooth that should normally replace it usually fails to emerge, no numerical anomaly results. [This condition will be discussed in the sequel (V).]

The dental system in certain Cebidae, in the Simiidae, and in the Hominidae is liable to a considerable degree of numerical variation; thus as many as 4% of examples of *Cebus* and *Ateles*, and 8% among the Simiidae present instances of supernumerary teeth. Detailed accounts are provided by Bateson (*Materials for the Study of Variation*), Magitot (*Anomalies du Système dentaire*), and in the exhaustive records, with an extensive bibliography



Fig. 189. Accessory upper tooth behind the first molar of a Chimpanzee. (Lübeck Museum.)

collected by De Terra (*Beiträge zu einer Odontographie der Menschen-Rassen*. Inaugural Dissertation, Zürich, 1905).

CANINE TEETH.

The canine teeth may be considered first. Few numerical variations are recorded here. A remarkable case of reduplication of the upper canine tooth on one side may be seen in the skull of an adult Gorilla in the Hamburg Museum. There is no question of the retention of the deciduous canine tooth in this case. Hrdlička (*Proc. of the United States National Museum*, Vol. XXXI. p. 560) figures a precisely comparable example in the lower jaw of an Orang-utan.



Fig. 190.



Fig. 191.

Fig. 190. An accessory dental mass (x) in the maxilla of a native of New Britain. (Mus. Anat. Cant. W. L. H. D. del.)

Fig. 191. Two accessory dental masses (x, x) in the maxilla of a native of New Britain. (Mus. Anat. Cant. W. L. H. D. del.)

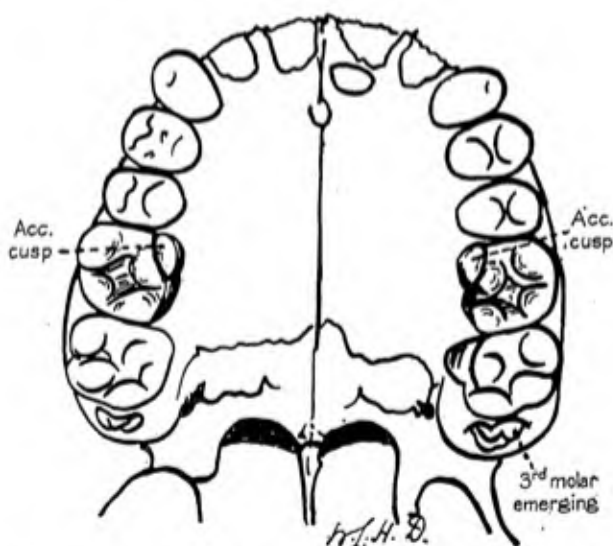


Fig. 192. Accessory cusps or tubercles of Carabelli in the molar teeth of an Egyptian. (Mus. Anat. Cant. W. L. H. D. del.)

PREMOLAR TEETH.

Additions to the premolar series of the Katarrhinae might be expected *à priori*, in view of the prevalence of three premolar teeth in the Platyrrhinae and lower Primates. Yet although an additional premolar tooth seems to be not uncommon in the Hominidae (Magitot, *op. cit.*, records a striking instance of supernumerary premolar teeth in the skull of a negro), such examples are rare among the Katarrhinae in general. De Terra¹ gives no instance of the kind. Yet, apart from complete accessory or supernumerary teeth in the premolar region, small dental masses (scarcely worthy of being described² as teeth) also appear occasionally in the crania of Simiidae and Hominidae. They are often seen between the second premolar and the first molar teeth in the upper jaw.

A good instance is the peg-like tooth shewn in Fig. 189 in the skull of a Chimpanzee. In the skull of a Gorilla, small dental masses occur in similar positions, as in that shewn in Fig. 193, where one small mass intervenes between the last premolar and first molar teeth, while a second occupies a corresponding place between the two premolar teeth. These masses are rare in the mandible whether of the Simiidae or Hominidae. In the former, the Gorilla provides the greatest number of examples, while among the Hominidae the crania of natives of Melanesia furnish more instances than any other group I have been able to examine³. Two examples from such crania are given in Figs. 190 and 191; it will be noted that in one case the dental masses are symmetrical, while in the other the anomaly occurs on one side only. The view that these

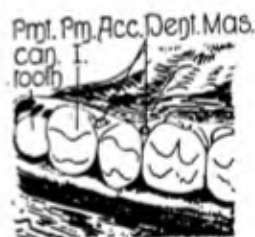


Fig. 193. Left upper teeth of a young Gorilla: accessory dental masses are situated between the first and second premolar teeth, and between the second premolar and the first molar tooth respectively. (W. L. H. D. priv. coll.)

¹ *Beiträge zu einer Odontographie der Menschen-Rassen*. Inaugural Dissertation, Zürich, 1905.

² Windle (*J.A. and P.* Vol. xxi. p. 84) distinguishes very appropriately between "supernumerary" imperfect teeth and "supplemental" teeth of size commensurate with those adjacent to them.

³ Cf. Duckworth and Fraser, *Proc. Camb. Phil. Soc.* 1900.

anomalous bodies are to be regarded as vestiges of teeth otherwise represented no longer in the normal dentition has been stoutly contested. Professor Dixon regards them as remains of deciduous teeth. Professor Adloff holds that they throw no light whatsoever on the phylogeny of the teeth with which they are associated. Those on the "lingual" side of the alveolar margin may possibly represent elements in a "post-permanent" dentition (*v. infra*, p. 275).

In connection with the "bilateral" occurrence of dental masses (cf. Fig. 191), it seems worth remarking that they occupy the

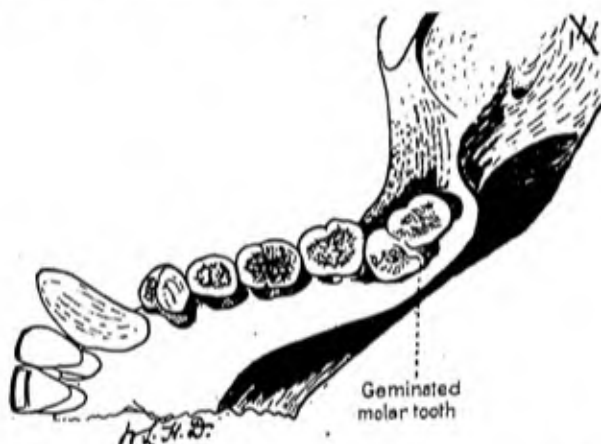


Fig. 194. Geminatio of the last molar tooth in the mandible of an Orang-utan. (Selenka Coll., Munich.)

position into which would come the accessory cusps shewn on the first upper molars in Fig. 192.

These accessory cusps represent the *tuberculus anomalus* of Carabelli¹. Besides the interest conferred on it by reason of its situation as compared with the dental vestiges described above, the tubercle of Carabelli is noteworthy for another reason. It is claimed by Batujeff (quoted by Osborn²) as distinctive of the higher rather than the lower human races. Adloff (quoted by Osborn, *ibidem*) considers that it is not found in the dentition of

¹ Cf. Bibliography in De Terra's *Beiträge*, 1905, under "Batujeff."

² *Evolution of Mammalian Molar Teeth*, 1907, p. 159.

the anthropoid apes. In spite of this, the tubercle need not indicate a progressive evolutionary phase, for Osborn identifies it with a cusp called by him the protostyle, and observed in many of the lower mammals.

MOLAR TEETH.

Additions to the number of molar teeth may be by way of gemination, of which a good instance exists in an European skull (from Paestum) in the University Museum of Anatomy, while a striking instance is shewn in Fig. 194, which represents gemination in the last molar tooth in the mandible of an adult Orang-utan. The original specimen forms part of the Selenka Collection at Munich.

Among the Anthropoidea, supernumerary molar teeth occur with some irregularity in the various "families" concerned. This statement arises from the consideration of the records collected by Zuckerkandl (quoted by De Terra, *op. cit.*).

Thus for instance in the Cebidae, the genus *Ateles* provides more examples than either of the genera *Cebus* or *Mycetes*. But in all these cases the accessory tooth is regarded as a fourth molar, and it is situated in the upper jaw.

Passing to the Cercopithecidae, again it appears that accessory molar teeth are very infrequent. The same remark applies to the Hylobatidae among the Simiidae, for no instance was observed in a collection of fifty-one crania of that genus.

The Orang-utan provides by far the greatest number of records among the larger Simiidae, the Gorilla coming next, and the Chimpanzee last in this sequence. Thus in the Orang-utan (cf. x, Fig. 195) the frequency of occurrence in the male sex amounts to nearly 50% (for the Gorilla the corresponding figure is about 8%).

This statement is based on the examination of the very large collection (more than 200 crania) at Munich, in the course of which the very remarkable example shewn in Fig. 196 was discovered. In this example four fully-formed molar teeth are seen: behind the last of these is an aborted dental mass, and behind this a depression which had probably contained yet another dental mass.

Since examining the specimens at Munich I find that Selenka in describing his collection has commented upon the remarkable frequency of the occurrence of additional molar teeth in male Orang-utans. Selenka states ("Rassen und Zahnwechsel des



Fig. 195.

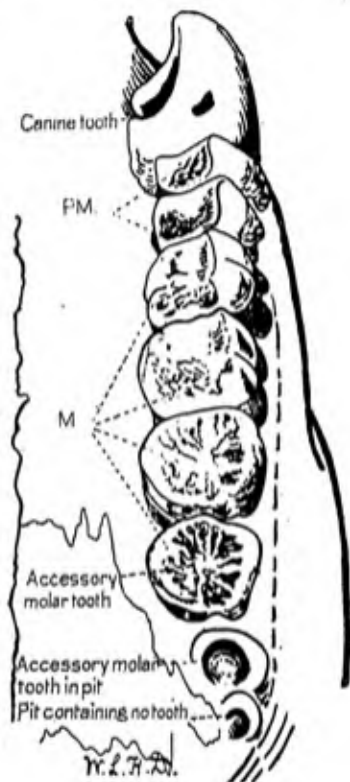


Fig. 196.

Fig. 195. Mandible of an Orang-utan (ad. ♂) with an accessory molar tooth (marked x) on the right side. (Hose Donation II. Mus. Anat. Cant.)

Fig. 196. Accessory teeth in the maxilla of an Orang-utan. (Selenka Coll., Munich.)

Orang-utan," *Sitz. der kais. preuss. Akad.*, Berlin, 1896) that the anomaly occurs in 20% of male crania. Other remarkable instances of supernumerary molar and other teeth in the Orang-utan are recorded in a paper by Hrdlička (*Proc. United States Nat. Museum*, Vol. xxxi., especially p. 558, Figs. 6 and 7).

It is perhaps worthy of notice that among the large anthropoid apes, the accessory molar teeth are found more frequently in the lower jaw than is the case with the Cebidae and lower Primates. This is especially true of the Orang-utan. But taking the three large anthropoid apes together, the upper jaw still provides a greater number of instances of the anomaly in question.

Completely formed accessory molar teeth are not common in the Hominidae, although the palate and alveolar arcade in many crania of aboriginals of Australia seem to be spacious enough to accommodate them. It is however in the cranium of such an aboriginal native that Sir William Turner records the occurrence of no less than three accessory molar teeth, and such anomalies are more frequent in the Melanesian and Australian aborigines than in other Hominidae.

INCISOR TEETH.

It remains to consider additions to the incisor series. Supernumerary incisor teeth constitute a large proportion of the anomalies of the human dental system, but as in the preceding categories, care must be taken to distinguish between veritable cases of accessory teeth and instances where the apparently supernumerary tooth is merely a retained tooth of the milk dentition. The distinction is not always easy to draw, and an instance of this is shewn in Fig. 197, where however the length of root exhibited by the supernumerary tooth is evidence against the case being one of retention (for the milk teeth are not so deeply rooted as those of the permanent series, and the root is subject to a process of phagocytic absorption which in fact leads to the ultimate separation of the deciduous tooth from its articulation).

In regard to other anomalous conditions of the incisor teeth, records of gemination (cf. gemination in the molar teeth, p. 260,

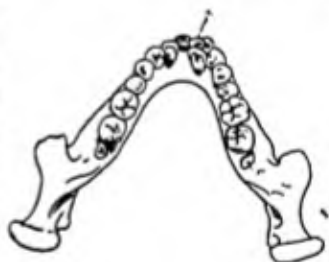


Fig. 197. Mandible of an aboriginal Australian, with a supernumerary incisor tooth. (Mus. Anat. Cant.)

and Fig. 194) of these teeth are noted by Windle (*J. A. and P.* vol. XXVIII. p. 374). A striking case is described (by Cameron¹) in the upper jaw of an ancient Egyptian, and other examples in the Hominidae will be considered in the sequel.

Supernumerary incisor teeth are of rare occurrence in the lower Anthropoidea, and the records become numerous only when the data relating to the three large anthropoid apes are studied. Again the Orang-utan heads the list with the greatest number of records, and as in the case of the molar series, the Gorilla comes next in order, followed by the Chimpanzee.

II. *Dental variation in form.*

Reference must be made first to the spatulate form of the upper incisor teeth in some of the lower races of Man, ex. gr. Negroes of Africa and Melanesia. This character is found in modified form in the corresponding teeth of the Orang-utan, and again in certain extinct Lemurs, ex. gr. *Nesopithecus*. Otherwise it can scarcely be claimed as providing evidence on the subject of human dental evolution. Indeed in the Oceanic-negro types mentioned above, it may well be the local representation of the general enlargement of the teeth which is so distinctive of some of those types. I am inclined to think that it is a character of comparatively recent development in the Hominidae².

"Gemination" of teeth is not included here for it is described in the preceding section. In the present place we have to consider the general form of the dental crowns, and the form and number of the roots. In a few instances, the roots of these teeth have been found reduplicated or bifid. The phenomenon of reduplicated roots is better dealt with in relation to the canine teeth in the next paragraph.

CANINE TEETH.

The canine teeth offer only two anomalous varieties for treatment here, but one of these is of very great interest. It consists in the reduplication of the root. This has been recorded in the

¹ Publications of the Manchester Museum, No. 68.

² Cf. Miklucho-Maclay, *Zeitschrift für Ethnologie*, Band VIII. : also Chapter XIV *infra*.

Hominidae with a moderate degree of frequency, and there is one record for *Cynocephalus* (De Terra, *op. cit.*, p. 269), but in no other of the Primates above the Lemurs so far as I am aware. As for the Lemuroidea, it is stated by De Terra (*op. cit.*, p. 241) that Professor Leche has recognized double-rooted canine teeth in the deciduous as well as the permanent dentition of those animals. At least three important points arise for consideration here.

(a) The mammals in which the double-rooted canine has been observed are:

- (1) Hominidae (as an anomaly).
- (2) Lemuroidea (? anomalous).
- (3) Certain Insectivora, ex. gr. *Microgale*¹; also *Galeopithecus* (normal).
- (4) Certain of the earliest fossil mammals, viz. *Diplocynodon*, of the Upper Jurassic (normal).

Thus it might seem that the double-rooted type of canine tooth is the original one. Yet Professor Gregory in admitting this possibility, gives a word of warning to the effect that the single-rooted canine is found in the same groups of animals and throughout just as great a range of geological time, as the more complex form.

(b) The occurrence of double-rooted canine teeth supports the view (attributed to Sir Ray Lankester by Professor Osborn, *Evolution of Mammalian Molar Teeth*, 1907, p. 194), that the canine tooth is really a modified premolar tooth.

(c) Among the Hominidae, canine teeth with double roots are peculiarly frequent in early British crania as contrasted with all others. This was noticed by Rolleston many years ago. The observation is confirmed by specimens in the Cambridge Collection, which includes a remarkable mandible (of mediaeval age) in which the right canine tooth has two roots, while the first premolar tooth (adjoining it) has but the normal single root.

The other anomaly of the canine teeth consists in the occa-

¹ Gregory, *Bulletin of the American Museum of Natural History*, Vol. xxvii. 1910, pp. 289, 290.

sional occurrence of accessory cusps, which have been observed in the Hominidae and in the Gorilla.

PREMOLAR TEETH.

Anomalous forms of premolar teeth provide few records. In the Gorilla there is on record one observation (cf. De Terra, *op. cit.*, p. 256) to shew that the second lower premolar has a tendency to become tricuspid. But the evidence is almost negligible, though it is at least noteworthy that the premolar nearest the molar series is the tooth concerned. Tricuspid premolar teeth are of common occurrence in the Hominidae, especially in the races (black and yellow) of Oceania (Choquet¹). They also characterize certain fossil mammalia, and such premolars have attracted much notice in connection with one of the theories (the "premolar-analogy" theory) advanced to account for the origin of the molar cusps.

In the Simiidae the upper premolar teeth have three roots, thus resembling the upper molar teeth in those animals and in the Hominidae. The occurrence of three-rooted upper premolar teeth in the latter (Hominidae) thus demands a special note. The presence of an additional root in these teeth is by no means unknown. The most striking example on record is probably that of the native of Timor (East Indian Archipelago) recorded by De Terra (*op. cit.*, p. 240). In this example the two upper premolar teeth of each side were found to possess three roots. Thus the condition normal in the lower Primates was precisely reproduced.

In dealing with the lower premolar teeth, De Terra (*op. cit.*, p. 241) cites an instance of a lower premolar with two roots, the condition commonly found in the lower Katarrhinae being faithfully represented in this example.

MOLAR TEETH.

Accessory or supernumerary molar cusps are of great interest in relation to the various theories of cusp-development. Such anomalies are therefore discussed in the section (VI) relating to those theories. Here it will suffice to mention that additional

¹ Choquet in *L'Odontologie*, Jan.-Fév. 1906, p. 21 of reprint.

cusps are of frequent occurrence in the molar crowns of the Hominidae and of the higher Primates in general.

But the molar teeth may also present anomalous conditions of their roots. In the Hominidae, additional roots are as likely to be found in the lower as in the upper molars. The number of accessory roots is variable, and in the third lower molar as many as three have been recorded (making a total of five roots). The socket for the third lower molar tooth in the celebrated Naulette jaw is said to indicate the former presence of a tooth with five roots. But this statement is not confirmed by the examination of a cast of this mandible (in the Cambridge Collection), nor is it supported by the photograph recently published by Dr Keith (*Proc. Roy. Soc. Medicine, Odont. Sect.*, Vol. vi. 1913).

Accessory molar roots in the other Primates are probably rare, for records are inaccessible or non-existent.

Reference must be made here to the remarkable and aberrant forms presented by some (but not all) of the prehistoric human teeth from the site at Krapina in Croatia (Fig. 198).

The outstanding feature is the fusion of the roots in the molar teeth. The combined roots form a pillar supporting the crown of the tooth. At the base of the pillar the extremities of the roots are in some examples indicated by small pointed projections. Between these projections, a plate-like or saucer-shaped disc (*Wurzeldeckel*) completes the fusion of the roots, and is very evident in a vertical section of the tooth (Fig. 198 K.o.). Teeth so anomalous as these offer a striking contrast to all other molar teeth in the Primates. As a rule the roots of the molar teeth in this group of mammals are distinctly divergent from one another.

Thus the Krapina type differs from the normal molar much as does the molar of the Ox from that of the Dog. For this reason, Professor Keith proposes to describe the Krapina molars (thus characterized) as "taurodont," while the normal type is designated "cynodont".¹ The same writer points out that in the taurodont molars, the pulp-cavity extends within the gum or alveolar margin of the jaw, whereas normally the pulp-cavity stands clear of that

¹ *Proceedings of the Royal Academy of Medicine*, Vol. vi. Odontological Section, 1913.

structure. The teeth so modified may be derived from either the upper or lower series.

Such are the principal features of these teeth. By way of comment it is permissible here to remark (*a*) that the analogy of the bovine tooth is only partial, since in that type the whole crown is enlarged and increased in vertical extent, the roots becoming or remaining quite short and the pulp-cavity failing to

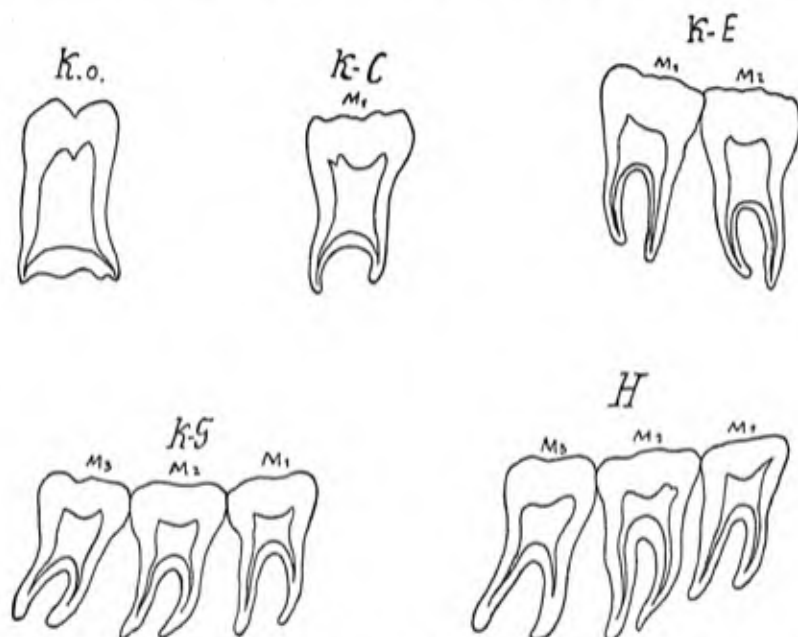


Fig. 198. Tracings (from skiagrams) of various molar teeth. The specimen K.O. (from Krapina) shows the conjoined roots characteristic of teeth found at Krapina, and in Jersey at St Brélade's Bay. The large pulp-cavity of the Krapina teeth should be noted. K.O., K.C., K.E., K.G., from Krapina. H. Mauer. (From Kramberger.)

extend towards the crown; (*b*) that the anomalous character of fusion is shewn (by Kramberger himself¹) to occur in modern human dentitions, so that its presence in the Krapina teeth is not absolutely distinctive; (*c*) that in spite of this last consideration, the frequency with which the molars especially the third or last of

¹ *Anat. Anz.* Band xxi. 1907, pp. 131, 132, 133.

these teeth presents this form in the Krapina specimens, added to the fact of its appearance in the palaeolithic human teeth from St Brélade's cave (in Jersey), leads to the conclusion that the character in question is decidedly distinctive of a definite variety, even if we deny to it the value of a specific character.

III. *Dental variations in situation.*

Displacement of teeth is rendered probable in cases in which the space available for their implantation is diminished without actual suppression of some of the teeth. This consideration provides an explanation of many cases of the occurrence of teeth in unusual situations, but is not altogether accountable for displacements observed in certain instances among the black races of the Hominidae, in which the jaws are large and the space extensive.

Again, the displacements observed in some skulls of Gorilla are evidently not attributable to the factor of maxillary (or mandibular) reduction.

The Anatomical Collection of Cambridge University includes examples of dental displacements in crania of aboriginal natives of Australia. In one such skull the canine teeth emerge on the facial surface of the maxilla, and their direction has been so altered that they lie in the horizontal rather than in the vertical plane. The same Collection contains the cranium of an ancient inhabitant of Peru, which presents a precisely similar condition of the same teeth. Again, the third molar tooth may emerge on the facial surface of the maxilla, immediately below the malar process: instances of this have been seen in an ancient skull from a cave in Jamaica: as also in the cranium of an aboriginal native of Australia (in the possession of Dr Haddon); while the same condition obtains in the skull of an Orang-utan in the Museum at Amsterdam.

The incisor teeth are subject to similar variations in position. Of these, perhaps the most striking are present in two crania from the Melanesian island of New Britain: in each of these specimens an incisor tooth has emerged, not on the alveolar margin of the maxilla, but on the lower margin of the apertura

pyriformis nasi: in each case, however, the tooth is imperfectly formed¹.

The occurrence of teeth, more or less perfectly formed, in dermoid cysts and ovarian tumours, must be regarded as beyond the scope of the present account.

IV. *Variation by reduction in the number of the teeth.*

This is rare, but not unknown in the Primates other than the Hominidae. In these, the numerical reduction is met with so frequently that a definite trend in evolution is suggested. It is possible that a similar process is affecting the Ateles type (South American monkeys) and even Hylobates.

Thus Ateles is characterized by the large number of anomalies to which its dentition is liable, and this includes a tendency to the loss of the last molar tooth (either in the upper or lower jaw)². This stage seems to have been reached by the Hapalidae (Marmosets). The Hylobatidae are said by Selenka³ to be on the way to lose not only the last molars but also the second premolar teeth. An unusual anomaly in the Orang-utan, viz. the absence of the third lower molar tooth, is recorded by Hrdlička⁴. Absence of an incisor tooth is on record in the case of several of the lower Primates, and in one instance in the skull of a Gorilla⁵. But evidence for a "reduced dentition" does not become striking until the Hominidae are reached⁶.

In Man and especially in the white races, the teeth first to be suppressed are the third molars, and there is a distinct tendency to the disappearance of the lateral incisor teeth. These changes have been attributed to the progressive reduction of the jaws, a

¹ A corresponding case was described by Goethe in the last century: cf. also *The Lancet*, Oct. 14, 1905, p. 1146.

² Bateson, quoted by De Terra, *op. cit.*, p. 286.

³ Selenka, v. De Terra, *op. cit.*, p. 286.

⁴ *Proc. United States National Museum*, Vol. xxxi. p. 539.

⁵ Regnault, quoted by De Terra, *op. cit.*, p. 286.

⁶ Reduction has proceeded to even greater length in the Aye-Aye (*Daubentonia* or *Cheiromys*). This Lemuroid is so aberrant from its associates, that it would not be profitable to discuss its dentition in detail here. The difference between the deciduous and permanent dentitions of the Aye-Aye is striking and very instructive.

process not yet arrested. That it is correct to hold the jaws accountable can scarcely be doubted in so far as the white races are concerned. But the occurrence of reduced dentitions in natives of Melanesia, where the jaws and even the remaining teeth are of great size, shews that some other factor is probably involved. Thus the dentition may be subject to an evolution in which the reduction of the jaws plays a subsidiary part only. Professor Röse is quoted by Dr Adloff as appealing to cerebral growth, which may indeed prove an important factor, though Dr Adloff does not agree that it is so¹.

We have seen that the dental formula of the Katarrhinae (including the Hominidae) shews a reduction in the number of the teeth as contrasted with that of the Platyrrhinae. At this stage it is convenient to enumerate and review the various formulae of interest in relation to the evolution of the human type.

Thus it will be found that the "primitive" mammalian dental formula allows for many more teeth than even that of the lower Primates.

Osborn regards that primitive formula as

$$(a) \quad I \frac{3}{4} \quad C \frac{1}{1} \quad Pm \frac{4}{4} \quad M \frac{3}{3}.$$

Oldfield Thomas and other writers give the formula as

$$(b) \quad I \frac{3}{4} \quad C \frac{1}{1} \quad Pm \frac{4}{4} \quad M \frac{3}{3}.$$

Brunsmann (quoted by Kükenthal, *Jahr. der Anatomie*, 1902) seems to have postulated a stage in human ancestry in which the formula was

$$(c) \quad I \frac{3}{3} \quad C \frac{1}{1} \quad Pm \frac{3}{3} \quad M \frac{4}{4}.$$

The Lemurine and Platyrrhine Primates² provide as their formula

$$(d) \quad I \frac{2}{2} \quad C \frac{1}{1} \quad Pm \frac{3}{3} \quad M \frac{3}{3}.$$

The Katarrhinae (including normal Hominidae) have as their formula

$$(e) \quad I \frac{2}{2} \quad C \frac{1}{1} \quad Pm \frac{2}{2} \quad M \frac{3}{3}.$$

¹ Cf. Adloff, *Z. f. M. u. A.* 1907, pp. 110 *et seq.*

² The Hapalidae (or Marmosets) form an exception to this rule, their dental formula being $I \frac{2}{2} \quad C \frac{1}{1} \quad Pm \frac{2}{2} \quad M \frac{2}{2}$.

While the human formula is tending (as described above) to become

$$(f) \quad I \frac{1}{2} \quad C \frac{1}{2} \quad Pm \frac{2}{2} \quad M \frac{2}{2}.$$

The comparison of the normal human formula (e) with the primitive formula (a) will shew that in human evolution a net loss amounting to two incisor, two premolar and five molar teeth has been experienced. With the exception of the canine teeth, each type (incisor, premolar, and molar) has been reduced in number, though the degree of reduction varies. In the attempt to trace the history of the reduced dentitions, the problems as to the particular teeth that are missing from each region have attracted much attention, though final conclusions have not been reached on several points. Thus in regard to the incisors, the literature of the subject shews that each of the three primitive incisor teeth, cf. formula (b), has been claimed as the defaulter. Even in the critical account furnished by Bluntschli in 1910¹, the question seems to be left an open one.

As regards I_1 (the median incisor tooth), it may be remarked that the wide interspace in the Lemurine dentition between the upper median incisor teeth is suggestive, and that a supernumerary incisor tooth is not infrequent in this situation. Gadow adopts this view (as, I believe, does Lydekker also); Elliot Smith has recently recorded, while the present writer has observed, instances of a supernumerary incisor tooth in the position indicated.

The view that I_2 is the missing tooth is supported by Turner, Albrecht, and Wilson and is based largely upon considerations of the arrangement of the incisor teeth in cases of persistence of the suture dividing the premaxilla and maxilla (hare-lip)².

Windle (*J. A. and P.*, Vol. XXI, pp. 84, *et seq.*) favours the view that I_2 has been suppressed; this view rests on the fact that the pre-canine space is a common locality for the occurrence of supernumerary teeth; while if it be granted that the characters of the teeth merge by insensible gradations into one another, the space

¹ *Vierter Jahrschrift der Naturforschenden Gesellschaft in Zürich*, Jahrgang 55/56, 1910, 1911.

² For expositions of this subject cf. Windle, *J. A. and P.*, Vol. XXI., and Tomes, *Dental Anatomy*.

in question is indicated as the probable site of the missing tooth which should provide the transition stage (at present lacking) between the definitely incisor and canine types of tooth-crown.

Passing from the incisor teeth to those of the premolar series, the results of protracted investigations are not very much more definite. In this instance, two teeth of the original four (cf. formula (a) or (b)) have to be accounted for. Agreement appears to be fairly general in regard to the first of those which have disappeared. For there is a consensus of opinion that it is the premolar immediately behind the canine tooth, viz. pm_1 . Thus three premolars are left, as in the Lemurs, Tarsii, and Platyrrhinae. Then another premolar tooth disappears, the resulting dentition being characteristic of the Katarrhinae. The answer to the enquiry, which of the three Platyrrhine premolars is absent from the Katarrhine (including the human) dentition, is not easy to give, because opinions are divided between pm_1 and pm_2 of the Platyrrhine series.

(i) On behalf of the former, it is claimed that inasmuch as a premolar immediately behind the canine tooth has already been lost (reducing the number from the four originally present to three), the process of reduction will affect the rest in sequence, viz. pm_1 of the Platyrrhine dentition. Professor Adloff indeed claims that of the four original premolars, three may be seen in Rodents to undergo degeneration from before backwards in succession¹. The problem might seem to be resolved therefore in favour of regarding the reduction as affecting the premolars in regular succession from before backwards.

(ii) On the other hand, those who incline to regard the third premolar of the Platyrrhinae as the excluded element, have to base their opinion largely on the instances of anomalous supernumerary additions to the Katarrhine series. These supernumerary teeth are sometimes small (*v. supra*, p. 258), and it is at least doubtful whether they can be justly claimed as "reversions."

But a better argument (in favour of the disappearance of the hindmost premolar) has been advanced by Professor Bolk², whose view is so ingenious and attractive as to demand special notice.

¹ Cf. Adloff, *Z. für M. und A.* Bd XI. Heft 2, p. 379.

² Koninklijke Akademie van Wetenschappen, Amsterdam, April 27, 1906.

It may be described as follows. Professor Bolk reminds us that the South American monkeys possess a deciduous dentition in which three molariform teeth occupy positions to which three premolar teeth succeed as the permanent dentition is completed. The permanent molars emerge behind these teeth. But the crucial point in the theory consists in the suggestion that in the Old-World apes and Man, two deciduous molars corresponding to the first two of the *Platyrrhinae* appear, while the third exists but is delayed in its appearance. Still it does make its way to the surface; it is called the six-year molar (in Man), and is considered commonly to be the first of the "permanent" teeth to emerge.

Furthermore, the theory of Professor Bolk postulates that while the first two deciduous molars are replaced (in *Platyrrhine* and *Katarrhine* Primates alike) by premolariform teeth, yet in the *Katarrhinae* the third "deciduous" molar owns no replacing tooth, the latter being suppressed. Finally it is suggested that the third permanent molar tooth of the *Platyrrhinae* is no longer present in the *Katarrhinae*.

If we apply all this to the permanent dentition of the latter forms (*Katarrhinae*), it follows that on the theory of Professor Bolk, the actual conditions observed involve (a) suppression of a molar tooth, viz. the last in the series of the *Platyrrhinae*, (b) the suppression of the third premolar tooth of the *Platyrrhinae*, and (c) delayed emergence of the third "deciduous" molar of the *Platyrrhinae*, which loses its "deciduous" character in consequence of the suppression postulated under (b).

The diagrams (Fig. 199 A and B) may serve to illustrate these suggestions more clearly, and although exhaustive discussion is not possible in this place, the support given by Professor Bluntschli, and the strong opposition of Dr Adloff demand mention. In spite of that opposition I agree with Professor Bolk that his suggestion makes no unreasonable demands upon the established principles of Odontology. That a tooth which is ordinarily deciduous may assume a permanent character is well recognized. Professor Leche has recorded such an instance in certain *Insectivora*, and Magitot states that the second (human) deciduous molar may persist while the replacing tooth fails to appear. Indeed this constitutes an exact repetition of the process postulated by Professor Bolk.

Professor Röse (quoted by Bolk, *op. cit.* p. 8 of reprint) has established the fact that the first permanent molar (in Man) develops precociously, at an early period, i.e. in relation to the deciduous rather than to the permanent teeth. Moreover, Professor Bolk points out that in the Platyrrhine monkeys known as the Hapalidae (Marmozets), the process described by him has affected the last molar teeth [assumption (a) *supra*] while it has not yet extended to the premolar region. Dr Adloff himself has pointed out the close relation of premolars and molars, suggesting that the differentiation of the premolars has proceeded from a more ancient (molar) type, and constitutes a modification of the primitive dentition¹. To this subject attention must now be turned.

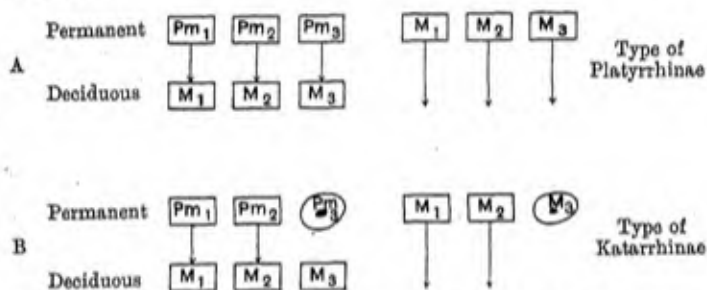


Fig. 199. Diagrams illustrating Professor Bolk's theory of the relations of the premolar and molar teeth in the Platyrrhine (A) and Katarrhine (B) Primates. In (B) the dental germs Pm₃ and M₃ (enclosed by oval contour lines) are regarded as failing to mature.

V. The evolution of the incisor and other types of teeth in the Primate dentition.

Before this subject is discussed the characteristic phenomenon of the replacement of one set of teeth by another demands further consideration here.

(a) We have seen that the teeth are, in the Primates, naturally divisible into four classes (incisor, canine, premolar, and molar teeth) for the most part easily distinguishable, though at the same time there may be seen, even in a single jaw, such as that of an

¹ For further information on this subject, reference should be made to the great work of Mr C. S. Tomes, *A Manual of Dental Anatomy*, 7th edition, 1914, especially pp. 337 et seq.

Orang-utan (*v. ante* Figs. 172 and 173), evidence of a transition in type from one class to another. Such animals as present these variations in their normal tooth forms are described as heterodont, and are hereby distinguished from homodont animals, the latter possessing teeth of one pattern only; and usually it is found that homodont teeth are present in large numbers disposed along an elongated jaw.

Again, the animals in which replacement of a deciduous set of teeth by a permanent series has been observed, are referred to as diphyodont, in distinction from monophyodont animals, in which but one set of teeth is seen. The Primates (including Man), and indeed most of the higher mammals, are heterodont and also diphyodont.

The Metatheria (Marsupials) appear to be monophyodont, but it has long been known that their most posterior premolar tooth is replaced: moreover Leche, Hill, and Wilson have discovered traces of other teeth which do not attain functional perfection. The Prototheria provide some evidence in the same direction, and in fact it is stated by Tims (*J. A. and P.* vol. xxxv., p. 321) that no mammal has yet been shewn to be absolutely monophyodont. Moreover, in addition to the two sets of teeth so characteristic of the Eutherian mammals, vestiges have been discovered of two other series, which may be described as constituting a "pre-milk" and a "post-permanent" set respectively. This discovery, which we owe to the work of Röse and Leche, has increased the complexity of the problem of deciding which sets of teeth are homologous in mammals of the various Sections: and in particular, the identification of the ordinary set of teeth of Marsupials is still a matter of controversy. It is also to be remarked that according to the respective researches of Tims and Röse, the human foetus possesses unmistakeable vestiges of representatives of both pre-milk and post-permanent series, and it is a characteristic feature of the abortive tooth-germs that the so-called pre-lacteal germs should be developed on the labial side of those germs which proceed to become functionally active, while the post-permanent representatives are placed on the lingual side of the permanent teeth.

In his exhaustive article in the *Bibliotheca zoologica* (Heft 17, 1895, Stuttgart), Leche remarks that in the four dentitions (which

he distinguishes by Roman numerals I—IV), the several elements develop as follows:

No. I. The teeth do not attain the stage of calcification, and are represented by vestigial buds only, situated upon the labial margin of the gum.

No. II is regarded as the ordinary "milk" dentition.

No. III is the ordinary permanent dentition.

No. IV. This series is usually represented by "buds" on the lingual side of No. III: these elements may sometimes arrive at maturity and appear as definite teeth. Subsequently (in the same memoir) Leche discusses the subject of the reduction in the number of functional dentitions. He suggests that the reduction was necessitated by the circumstances under which the mammalia were evolved from pre-mammalian reptilian ancestors; that however, only dentitions I and II have been inherited from such ancestors, III and IV being newly evolved and peculiar to the mammalia. This position is not quite easy to grasp in view of the fact cited by Beddard (*Mammalia*, p. 53), that Leche has himself described in a reptile (*Iguana*), no less than four series of teeth which reach maturity, while a rudimentary (or vestigial) series, antecedent to these, never produces fully formed teeth.

But in the memoir quoted, Leche defends his position that new dentitions can arise, though he recognizes the objections that have been adduced by Kowalevsky, Schmidt, and Schlosser. Finally, in a more recent memoir (*Bibliotheca zoologica*, Heft 37, 1902) upon the dentition of the *Insectivora*, Leche brings forward further evidence in support of the foregoing view.

These discoveries of a number of dentitions, some of which are recognizable in the *Hominidae*, detract to some extent from the value of Schwalbe's review of the subject as presented to the German Anatomical Society in 1893. Nevertheless that address still retains all its historical interest, and includes certain remarks which may here be briefly recapitulated. In the first place, Schwalbe points out the difficulty in determining criteria for the several series of teeth. He quotes Leche as pessimistically admitting that such criteria are not to be hoped for, though the same author clearly indicates that he regards each dentition as a

tooth-generation. This question of the criteria is still a matter of discussion (*v. infra*, p. 291, footnote). Schwalbe emphasizes the significance of the independence of the milk and the permanent series as regards their original positions, and this independence would seem to be extended to the other dentitions subsequently discovered. A large part of the memoir is devoted to a discussion as to whether the ancestral mammals had one or two dentitions, but this part of the question is of course no longer relevant, except as regards one point. For in drawing up a table of the several schemes which have been devised to shew the originator's views regarding the relations of the permanent to the milk-teeth, Schwalbe shews that he regards premolar and molar teeth as derived from conjoined elements from the two dentitions (*v. infra*, p. 295). Kükenthal has, I believe, shewn evidence of such a coalescence in a special instance, but otherwise the subject has not been finally decided.

The history of the evolution of the several series is thus to a large extent obscure: the general significance of the replacement of one dentition by another must evidently be found in the advantage therefore conferred on the animal, which is thus able to bring series after series into use, as the preceding set is lost or worn away. And whether two, or all four of the dentitions recognizable in the Hominidae, are inherited from ancestors in the reptilian phase or not, the general conclusion must be that the multiple dentition has been inherited from polyphyodont ancestors, and has subsequently been modified in accordance with the special needs of this family of the Primates.

(b) In the endeavour to explain the origin of the different forms of teeth, such as the incisor, canine, and molar series, in other words in the attempt to render a clear account of the historical development of the heterodont dentition, some investigators would refer all the various forms of teeth back to a simple ancestral parent-form; and the simplest form known is the conical¹ peg-like tooth found repeated in series with practically no variation (homodont)²,

¹ It appears that Rüttimeyer first suggested that the conical tooth represents the ancestral form, cf. Forsyth-Major, *Proc. Zool. Soc.* 1893.

² Leche, *Bibliotheca zoologica*, 1895, demurs to the view that the homodont condition is the original mammalian one.

throughout the length of the slender jaws of the Odontoceti or toothed whales. Moreover the reasonableness of this view seems enhanced by the fact that many reptiles (and a reptilian stage is postulated in the most widely-accepted view¹ as to the ancestry of the Mammalia, cf. the scheme in Chapter III. p. 37) possess such simple teeth, which are often described as haplodont. Most



Fig. 200. Molariform teeth of fossil reptile *Diademodon*. These teeth were implanted in sockets, and in their general appearance are mammalian. (After Osborn.)

reptiles are also homodont, and it was from these, and not from the rarer heterodont reptiles, that Cope traced the Descent of Mammals (cf. *Factors of Evolution*, p. 331). It is noteworthy that in many reptiles the teeth are ankylosed with the jaws, whereas in mammals the teeth are *thecodont*; they are implanted in sockets, this being a form of articulation (not an ankylosis) known as Gomphosis. The difference between mammals and reptiles in this respect is not however absolute, for the Crocodilia are thecodont, and so was the extinct reptile known as *Diademodon*. (Cf. Fig. 200.)

¹ The fact must not be ignored that certain observations suggest a direct origin of the Mammalia from the Amphibia, reptilian ancestors being thus omitted from the direct line of descent. This view is losing ground at present. (Cf. footnote 4, p. 279.)

Other palaeontologists objected to this exclusion of the heterodont reptiles from the ancestral history of the mammals. They pointed to the remarkable characters of some extinct reptiles known as the Theriodontia¹, and referable to the Triassic period. The last ten years have seen great accessions to our knowledge of those animals and it is almost impossible to resist the conclusion that the mammals passed through an ancestral stage corresponding to that of the Cynodontia (a particular sub-order of those fossil reptiles). Detailed evidence is accessible in the exhaustive memoirs published by Dr Broom².

A representation of the skull of one of the Cynodontia, viz. *Sesamodon browni*³, is shewn in Fig. 201. The skull of this Triassic

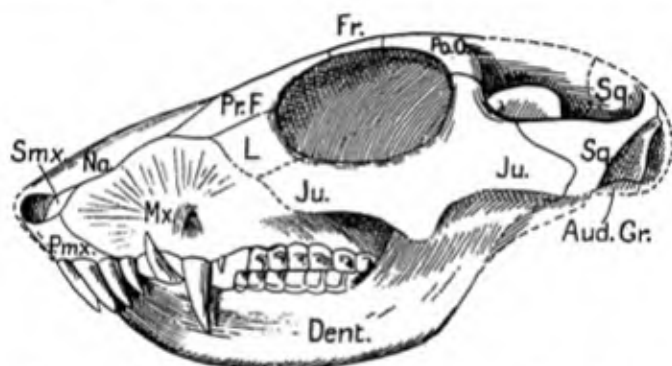


Fig. 201. Skull of *Sesamodon browni*, a Triassic reptile having a dentition similar to that of a mammal. (After Broom.)

reptile exhibits clearly the chief point of interest in the present connection, viz. that the reptilian dentition was already heterodont, to the extent that incisor, canine and post-canine types of tooth can be easily distinguished. In some of the Cynodontia, a distinction can be drawn between the pre-molar and the molar series also⁴.

¹ Cf. Woodward, *Vertebrate Palaeontology*, p. 247.

² Not the least striking result is the demonstration (Sept. 1913) of a deciduous dentition (in a Cynodont skull) resembling that of Mammals.

³ Cf. Broom, *P.Z.S.* 1911, p. 893.

⁴ The Cynodontia also serve to discountenance a view of the ancestry of mammals which at one time gained some support. That view excluded a reptilian stage, and carried back the mammalian line directly to an "Amphibian" stage to

The statements set forth in the preceding paragraphs tend to show:

(A) That the theory which regarded the conical teeth of the Odontoceti or Toothed Whales as the parent form must be modified, and indeed there is good reason for regarding the homodont haplodont dentition of those cetaceans as a secondary acquisition¹.

(B) That although the mammalian teeth are ultimately referable to a haplodont type, yet this must be sought for in ancestors more primitive than those to which the Cynodonts point, and in a geological period more remote than the Trias. Possibly the stage required is revealed in the Permian Cotylosauria. Osborn (1907, *op. cit.* p. 39) states that the haplodont type has not yet been discovered among the primitive mammalia.

(C) That the Cynodontia provide evidence to the effect that the distinction of incisors from canines, premolars and molars was brought about in a pre-mammalian stage, so that the evolution of those varieties must be sought in a correspondingly remote geological period.

the exclusion of a distinctively reptilian one. Such a view might be justified so long as the mammalian characters of the Cynodontia were unknown or not realized. By the recent extension of knowledge, the mammals are shewn to have emerged from an ancestral stock which they shared with the Cynodontia in so remote a period as the Trias. Gregory (*Bulletins of the American Museum of Natural History*, Vol. xxvii. pp. 117 *et seq.*, and *Journal of Morphology*, Vol. xxiv. 1913) has published invaluable summaries of the evidence on this subject. Cf. also *Rep. Brit. Assoc. Adv. Sc.*, Portsmouth, 1911, "Discussion on the Origin of Mammals."

¹ The toothed whales (possessed of a homodont and haplodont dentition) were at one time thought to lack a milk set of teeth, and were accordingly regarded as monophyodont; but Kükenthal's researches shew that they are really heterodont and also diphyodont, the first or "milk" set appearing as the normal teeth of these animals, while the second set of teeth is vestigial only. Moreover, Kükenthal (cf. *Denkschr. der med. naturwiss. Ges. in Jena*, Band iii. 1893, quoted by Schwalbe; *Anat. Anz.* 1894; also *Jenaische Zeitschr.*, Band xxviii. 1893, p. 76) found that even whalebone whales are provided with tooth-germs which early abort. These researches, together with those of Leche, indicate that the whales are the descendants of ancestors provided with more complicated teeth than those of the toothed-whales, and Kükenthal supposes that the numerous conical teeth of the latter result from the splitting up of several compound teeth. This suggestion is however by no means generally accepted, and in particular, Osborn and Gadow reject it. It should be added that Osborn (*Evolution of Mammalian Molar Teeth*, 1907) is quite ready to assent to the view that the haplodont dentition of the Toothed Whales is the result of secondary modifications in teeth of more complicated form.

Before leaving the Cynodontia, two more features must be noticed.

The dental formula is extraordinarily similar to that postulated by Osborn for the ancestral form of mammalian dentition, viz.

$$I \frac{4}{4} \quad C \frac{1}{1} \quad Pm \frac{4}{4} \quad M \frac{8}{8},$$

with which we may compare

$$I \frac{3}{3} \quad C \frac{1}{1} \quad Pm \frac{4}{4} \quad M \frac{7}{7},$$

the probable formula for the Cynodont form *Diademodon*.

Again a very early mammalian type (*Dryolestes*) from strata of the Jurassic period provides a mandible with the formula

$$I \frac{4}{4} \quad C \frac{1}{1} \quad Pm \frac{4}{4} \quad M \frac{8 \text{ to } 9}{8 \text{ to } 9}.$$

Lastly, the relation of upper and lower post-canine teeth is a matter of great importance. In the Cynodontia, as in the



Fig. 202. Dentition of an aboriginal native Australian woman, shewing the alternation of the teeth in the upper and lower jaws. This figure should be compared with Figs. 149 and 201. (From Skull No. 2115, Mus. Anat. Cant.)

Jurassic *Dryolestes*, the upper and lower teeth alternate. Thus each tooth in the upper jaw comes down behind the posterior border of the lower tooth, between it and the following one. Or, as in *Sesamodon*, an upper tooth rests partly on each of two of the lower crowns. Such alternation is clearly therefore the ancestral or primitive mode, and as it has been retained in many of the Primates, its significance is very great. In the *Hominidae* (Fig. 202), such alternation is shewn by Choquet (*L'Odontologie*, 1908, Jan. Fév.) to exist, but only in a minority of instances (38%). But the early establishment of such alternation in the phylogeny of the mammalian types is of the first importance, inasmuch as the development of secondary cusps has been determined thereby to no small extent. This subject will demand closer attention in the next section (VI).

These considerations have carried us away from the dentition of the Primates, yet on returning to consider their dental formula, we find that they retain the four great orders of teeth found in the Triassic reptiles. The differentiation of those orders (incisors, etc.) must have taken place at an earlier period, and must be ascribed partly to mechanical influences, such as the size and arrangement of the muscles acting on the mandible¹. Not less effective however were physiological influences, with which modifications of diet are connected. Alteration in the size and form of the jaw was determined by these and to some extent also by the increasing size of the brain. Of such factors, some were more active than others at particular periods of the evolutionary history. In the Primates, that factor which we denote generally by brain-growth persisted and at length predominated. Coincidentally the jaws became reduced in antero-posterior extent, and with this reduction the suppression of teeth was brought about so that the dental formula was at length established as we now know it.

VI. *Theories of cusp-development and the origin and fate of cusps.*

In the incisor and canine series the change from a (? original) "haplodont" form has been comparatively slight, though whether the result has been determined by natural selection, or "use-inheritance," would lead to a discussion upon which we cannot enter here.

But in the premolar and molar series the difficulties are greater: for the problem is to determine the origin of complex many-cusped teeth with multiple roots, from conical teeth with single roots.

The explanations which have been offered may be grouped under three chief heads: viz. the hypotheses of Trituberculy, of the Polybunodont origin of the teeth, and the hypothesis advanced by Marett Tims, with which the Concrescence theory will be considered.

It must be at once stated that no one hypothesis covers all

¹ Cf. Gregory, *Bulletins of the American Museum of Natural History*, Vol. xxvii. p. 111.

the cases, and hence it is necessary to enter into brief notices of each.

The tritubercular hypothesis is inseparably connected with the names of two American palaeontologists, viz. Cope and Osborn¹, and it is interesting to note that the theory is largely a generalization from the experience of extended investigations of the characters of fossil teeth. It was considered applicable to the molar teeth of both jaws (upper and lower) and to the lower series of premolar teeth; but not to the upper premolar teeth.

The theory has had an eventful history since Cope first expounded it some thirty years ago (1883). It has been extended and modified. Certain details have been abandoned as a result of the progress of anatomical and palaeontological science. The

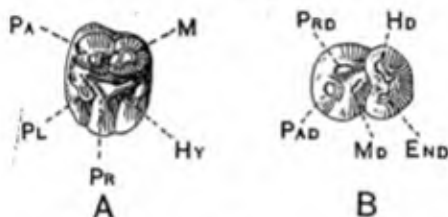


Fig. 203. Molar teeth of *Peripitychus*. A, upper; B, lower tooth. (From Osborn.) The three "primitive" cusps in the upper tooth are labelled Pn (protocone), PA (paracone), and M (metacone) respectively. In the lower tooth (B) the three "primitive" cusps are distinguished as PnD (protoconid), PAD (paraconid) and MD (metaconid), the names in parentheses having been devised by Cope.

essential parts of the theory have also been misapprehended, but in the brief sketch which follows, I have made every endeavour to present a fair account derived from the original sources so far as possible.

(i) As a conception, the Tritubercular theory seems to rest upon Cope's recognition of a remarkable feature in the teeth of certain very ancient fossil mammals found in New Mexico (Puerco Eocene). The animals themselves are assigned to the earliest subdivision of the Tertiary period (Basal Eocene). The peculiarity thus observed consisted in the fact that the molar teeth commonly presented three cusps arranged at the angles of a triangle (Fig. 203).

¹ Cf. Cope, *Primary Factors in Evolution*; Osborn, *American Naturalist*, 1888, p. 1074; *ibid.* 1893 and 1897; *Evolution of Mammalian Molar Teeth*, 1907; Gregory, *Bulletins of the American Museum of Natural History*, 1910.

Later research has shewn that this statement is too general, since minute cusps may and do supplement the principal prominences first observed (cf. Fig. 203 PL, HY, HD, and END). And again the difference in form between the upper and lower teeth is considerable¹. But even with these objections, the generalization was supported as being justifiable².

(ii) Fossil mammals of even greater antiquity than those of the Basal Eocene beds of Puerco were known even when Cope first advanced his theory. On examining the fossil remains of the Mesozoic (Jurassic) mammals, Cope arrived at the conclusion that the three-cusped tritubercular type of molar tooth observed by him, had arisen from a tooth of simple conical form (haplodont) by the addition of lateral denticles (Fig. 204).

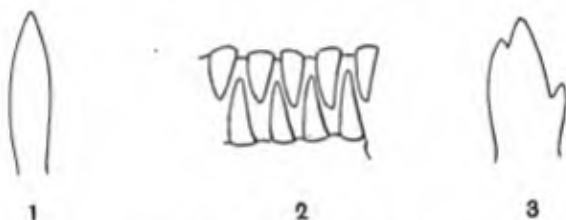


Fig. 204. Diagram shewing the derivation of a tritubercular (triconodont) tooth (No. 3) from a simple cone (No. 1). No. 2 shews the primitive alternation of upper and lower teeth. No. 3 is a tooth of *Dromatherium*. (From Osborn.)

(iii) Then it became necessary to account for the presence of these denticles. Cope supposed that they arose from the original undivided cone. This view has been greatly disputed. The most important alternative is embodied in a view which is distinguished as the theory of Concrescence. The name of Dr Röse is specially associated with this theory. It postulates the fusion of a number of simple cones situated originally in close proximity to each other. The theory of Concrescence is discussed in the sequel, and will not be considered further here.

¹ Gregory points out that the upper teeth have three cusps and belong to a type since termed tritubercular; the lower molars represent a modification of that type known as the tuberculo-sectorial variety.

² Matthew, *Bulletins of the American Museum of Natural History*, Vol. xxxi. 1912, pp. 307-314, lays stress upon the great antiquity of the triangular type of molar tooth, as exhibited by the Puerco Eocene Insectivore *Palaeoryctes puercensis*.

(iv) Assuming that lateral denticles had been added to a primitive cone, the next search was directed towards identifying the original cusp in the upper and lower teeth respectively. Cope (followed by Osborn in this particular) suggested that the "lateral denticles" were "rotated" from the sides of the original cone, and passed into new positions (Fig. 205).

An important point is that the rotation was supposed to have occurred in precisely opposite directions in the upper and lower teeth respectively. In the upper and lower teeth alike the cusps came to rest at the angles of a triangle (cf. Fig. 205 D), but the arrangement differed slightly in the upper and lower series inas-

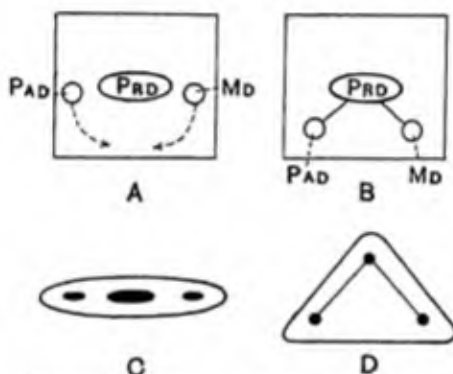


Fig. 205. A and B, diagrams of lower molar teeth to illustrate the process of cusp rotation. C and D, diagrammatic representations of the lower molar teeth of ancient fossil mammals bearing a similar relation to each other. C, tooth of *Dromatherium*, D, tooth of *Peralestes*. (After Osborn.)

much as in an upper tooth two cusps were external (buccal) and one cusp internal (or lingual) in position, while the cusps of the lower teeth were placed so that one was external (buccal) and two internal in position. This part of the theory is very important, for the identification of the original cone (in a given tooth) depends directly upon it. And consequently, identification is still possible even when the original cone has lost its superiority in point of size. The final relations of an upper and a lower molar tooth are shewn in the following figure (Fig. 206).

(v) The same illustration (Fig. 206) reveals another point of importance, viz. that the teeth alternate in the upper and lower

series when opposed, while the upper series as a whole are slightly external to the lower set. This condition has been termed anisognathism.

(vi) The final generalization laid down that the tritubercular type was ancestral to many if not to all the higher types of molar teeth.

Should the foregoing statement be accepted as a fair exposition of the theory of Trituberculy, its rejection clearly cannot be accomplished by the disproof of any single one of its sections. It is reasonable therefore to enquire into the position of each of these at the present time. They will be reviewed accordingly in the same order as that in which they are stated above (p. 283).

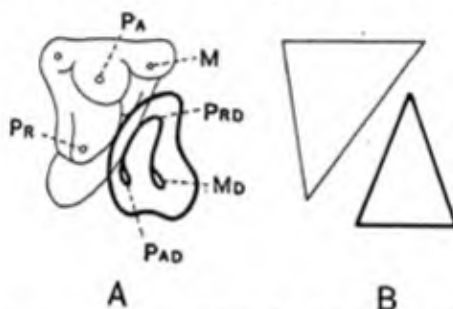


Fig. 206. The upper and lower molars of *Dryolestes*, an extinct and primitive mammal. The upper molar is drawn with a faint contour. The original cone Pn of the upper molar tooth occupies an "internal" position with reference to its two subsidiary cusps (PA and M), while in the lower tooth the original cone is now external. Upper and lower teeth alternate. (After Gregory.)

(i) This is a matter of observation, and as regards the Basal Eocene *Amblypoda* it still holds good, even though those mammals are not now accorded the "ancestral" status that Cope would have assigned to them. As a matter of fact the most ancient of known mammals (the Upper Triassic *Microlestes*) is not "Tritubercular" but "Multitubercular" in respect of its molar teeth (Fig. 208).

(ii) The evolution of the molar teeth from a simple conical or haplodont precursor still appears likely, though the haplodont stage in mammalian ancestry must be anterior to that represented by the Theriodont reptiles, and in point of time must fall in the earlier part of the Triassic period.

(iii) This section of the theory of Trituberculy is admittedly menaced if not actually overthrown. Osborn (1907)¹ maintained that the balance of evidence favoured the Tritubercular Theory. In 1910, Gregory² stated that in his opinion the view may still be correct that all the accessory parts are the offspring of a main protocone, the tip of which lies on the inner side of the upper, and on the outer side of the lower molars.

(iv) Rotation of the lateral denticles. This suggestion has been abandoned through lack of evidence. The objection based upon embryological grounds has been mentioned already. It seems undeniable that embryologically the cusp first developed is not the protocone, as should be the case in accordance with the hypothesis (cf. Taeker, quoted by Osborn, *Am. Nat.*, 1893; Woodward, quoted by Tims, *J. A. P.* xxxvii. p. 137; Tims, *op. cit.* p. 137; Heischmann, quoted by Röse, *Anat. Anz.* Band VII. p. 394; and Röse, *ibid.*), nor does there seem to be any embryological evidence of the circumduction (often spoken of as the rotation) of the secondary cusps.

It might thus seem that the objections are directed from the side of embryology only, but Tims (*op. cit.* p. 138) claims that the evidence of palaeontology is by no means flawless.

That the triangles of cusps bear a "reversed" relation to each other is however still maintained. Professor Gregory in 1910 expressed the opinion that the trigon (or triangle) above and the trigonid below may still be morphologically reversed structures.

(v) As a matter of observation, this part of the subject has undergone no modification.

(vi) This conclusion has been notably modified. Instead of making an appeal to the Tritubercular type (as defined above) as the ancestral one, the following terms are substituted (by Professor Gregory, *Bulletins of the Geological Society of America*, Vol. XXIII. June, 1912, p. 192): "There can now be very little doubt that many or perhaps all placental orders at one time passed through a stage in which the upper molars were trigonal, the lower tuberculo-sectorial." It is noteworthy that this description of upper molars

¹ *Evolution of Mammalian Molar Teeth*, p. 3.

² *Bulletins of the American Museum of Natural History*, Vol. xxvii. p. 184.

as trigonal and of lower molars as tuberculo-sectorial is really and actually a more precise account than Cope¹ himself gave of the molar teeth of the Puerco mammals upon which he originally founded his theory. (Cf. Fig. 203.)

The most recent modifications of the Tritubercular theory having been reviewed, we may now enquire how far it applies to the teeth of the Primates.

The Lemurs present no difficulty at all as regards the upper molar teeth for these are clearly tricuspid or tritubercular (cf. Fig. 161). *Tarsius* shews the same form (Fig. 163). In the Anthropoidea four cusps are found; the original triangle has thus an accessory cusp. Comparisons of various types and study of the variations in the individual teeth shew that the additional cusp is the postero-internal one, which as mentioned above (p. 244, footnote) is termed hypocone². The human upper molar teeth resemble closely those of the other Primates in this respect (Fig. 207).

The lower molars are not so easily explained. In the Lemuroidea (Fig. 162) the first of these bears five cusps which we meet again in the higher Primates. *Tarsius* retains the primitive form (cf. Figs. 164 and 203 B). In the human lower molars, we find the cusps disposed as shewn (Fig. 207). Reference to extinct forms shews that the "original" lower triangle or trigonid has lost a cusp, called the paraconid³. The other diagrams in Fig. 207 shew the different parts of the original trigonid and also those of the talonid or heel. The latter bears three cusps marked respectively HYD, HLD, and ENT. D (the Hypoconid, Hypoconulid and Entoconid of Osborn), though one of these, viz. the Hypoconulid (HL) is often wanting. These three cusps constitute the "talonid."

¹ *Evolution of Mammalian Molar Teeth*, p. 2.

² It is convenient to note here that the four-cusped arrangement seen in the upper molars of the higher Primates, was regarded by Cope as representing a comparatively early stage in the history of the complicated molar teeth of the Ungulata (especially evident in the Condylarthra) and even of the Proboscidea (*Moeritherium*). Herein may be recognized a suggestion of parallel lines of evolution.

³ This conclusion is based on the examination of the teeth of an extinct Primate, viz. *Anaptomorphus*. Cf. Osborn, 1907, Fig. 38.

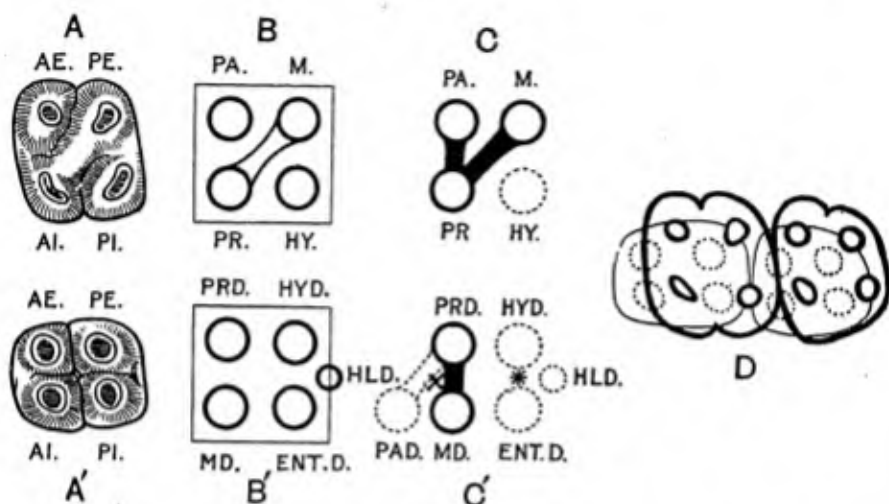


Fig. 207. Human molar teeth and their adjustment.

- A. Second upper molar tooth with four cusps.
- B. The same shewing the identity of the cusps, and the oblique ridge joining PR and M.
- C. The same, shewing the original triangle, to which the cusp HY has been added in Man.
- A'. Second lower molar tooth, with four large cusps and a small intermediate cusp posteriorly.
- B'. The same, shewing the identity of the cusps.
- C'. The same, shewing that the cusps marked PRD and MD are regarded as remnants of a triangle previously formed here, while the other three cusps (HYD, HLD and ENT. D) have been added¹.
- D. Tracings of the second and third upper molar teeth (marked by thick contour lines) superimposed upon the second and third lower molar teeth. (From the skull of an aboriginal Australian.)

Other indications :

AE. Antero-external cusp.
AI. Antero-internal cusp.
PE. Postero-external cusp.
PI. Postero-internal cusp.
PR. Protocone.
PA. Paracone.
M. Metacone.
H. Hypocone.

PRD. Protoconid.
PAD. Paraconid.
MD. Metaconid.
HYD. Hypoconid.
HLD. Hypoconulid.
ENT. D. Entoconid.

The Hypoconid, Hypoconulid and Entoconid together constitute the "talonid."

In C' the mark x shews where the Hypocone of the upper tooth should fall when the teeth close. The asterisk (*) shews where the Protocone of the upper tooth should fall in the same conditions.

¹ Transverse ridges connecting the cusps PRD and MD, and again HYD and ENT. D, are very distinct in the Cercopithecidae and are noticed in the description of the teeth of those animals (*v. supra*, p. 244).

But comparison with the "tuberculo-sectorial" type of lower molar as shewn in Fig. 203 shews that the human lower molar is very closely similar to that type, which (as noted above) is regarded as an "ancestral" one.

Similar remarks apply to the other Simiidae, to the Primates generally, and to *Tarsius* especially.

One prominent fact brought out by the study of these teeth as carried out on the lines suggested above, is that supplementary parts (hypocone above and talonid below) are appended to a triangle of cusps. The significance of these appendages seems to find an explanation when the teeth are shewn in adjustment. When the upper and lower teeth are thus adjusted, as shewn in Fig. 207 D, it will be seen that the "talonid" of the lower molar extends beneath the protocone of the upper tooth, while the hypocone or upper appendage comes down upon the primitive lower triangle or trigonid. At this stage we must remember the important point made in connection with the Tritubercular theory as first stated, viz. that the primitive triangles alternate in the upper and lower jaws. The appendages just described (viz. hypocone and talonid) represent the means by which the vacant spaces (alternately above and below) are filled so that the whole apparatus becomes a more efficient instrument. In fact it meets the need imposed by the change in function of the jaws from a comparatively simple prehensile apparatus to a mechanism for fine trituration and division of the food prior to its being swallowed. The origin of all parts accessory to the primitive cone is almost certainly dependent upon that need and the method of its realization. The precise manner in which the transformation has been effected is as yet unknown, but the "wedge-theory" proposed by Dr Gregory in 1910¹ provides at least a basis for research and a reasonably suggestive sketch of what has actually occurred. This brief statement must suffice here, since detailed discussion of the mode of origin of accessory cusps is precluded in this place. In conclusion, I may point out once more that the molar dentition of the Primates including that of the Hominidae, must be placed in a position close to that of the type claimed as distinctive of the ancestral mammals.

¹ *Bull. Am. Mus.*, 1910, pp. 184 et seq.

Turning from the molar to the premolar teeth, it may be repeated that Professor Osborn claims that the Theory of Trituberculy applies to the lower series, though in regard to the upper premolars, a most important difference has to be admitted. The difference is important because it has been held to throw doubt on the validity of the Theory of Trituberculy. The case of the upper premolar teeth therefore requires special attention. The upper premolar teeth appear to be derived from a conical haplodont tooth similar to the presumed original form of molar tooth. Professor W. B. Scott¹ observed three stages in the evolution of the most complex form of upper premolars. To the primitive cone three cusps are added in succession. They are derived from the cingulum and herein consists the first point of contrast² with the molar teeth, since in the latter the earlier accessory cusps are believed to arise from the sides of the primitive cone or from its base (cf. Fig. 204). With the addition of one cusp the first or bicuspid stage is reached and beyond this we need not pass since this is the ordinary type in the Primates. But the real difficulty of the situation is now to be presented and it consists in the fact that the second cusp (i.e. the first accessory cusp) makes its appearance on the *inner* side of the primary cone (protocone). But this is exactly contrary to what should happen if the process resembles that claimed for the upper molar teeth on the Tritubercular Hypothesis, for *ex hypothesi* the upper protocone itself should occupy that "internal" relation to the other cusps. But the evidence of embryology is very relevant here, since it testifies that of the two comparable cusps of the upper molar teeth, again the outer is the "older," although again the theory demands the converse. In the tritubercular molar and on the Tritubercular

¹ *Proc. Acad. Nat. Sc. Phil.* 1892, pp. 405—444, quoted by Osborn, *Evolution of Mammalian Molar Teeth*, 1907, p. 195.

² The point is of importance, because there is a difficulty in defining the exact difference between a molar and a premolar tooth. The Horse presents a notable case in point. The older writers seem to have believed that whereas the premolars are preceded by milk teeth, the true molar teeth are not so preceded. Difficulties in the applicability of this criterion having arisen, a difference in developmental history was somewhat eagerly seized upon as an alternative test, but this in turn seems to be a controvertible point, in view of the researches of Marett Tims (cf. *J. A. P.* xxxvii. p. 146).

Hypothesis *no* cusp is internal to the protocone. Professor Osborn realizes this and points out that the premolar "deutero-cone" (first accessory cusp) is not homologous with any molar cusp. And the same conclusion applies to the remaining premolar cusps. On the whole therefore, the study of the upper premolar teeth introduces a further element of uncertainty in the Theory of Trituberculy as originally stated. And these considerations fortify the position of those who believe that the premolars give the key to the history of the molar teeth; that the molars originally evolved as the premolars did at a later stage; and that the lack of agreement described above is to be regarded as militating against the Tritubercular Theory, and not (as Professor Osborn believes) as merely indicative that the upper premolars have evolved differently from the molars.

The view here taken is that the ultimate solution of the problem of molar and premolar evolution will owe much to the Theory of Trituberculy, but that theory will require even more modification than it has yet experienced before it can claim to hold the field to the exclusion of its rivals, and before all the existing objections have been dismissed.

Of the rival theories, three will be considered briefly. A. The "Premolar-analogy" theory of cusp-development. B. The theory of Multituberculism. C. The theory of Concrescence.

A. The "Premolar-analogy" theory is thus the first rival of the Tritubercular Theory to be enumerated. It is based largely on the work of Scott (quoted above), and it postulates the origin of cusps from the cingulum. In its favour are the difficulties (just described) in the application of the Tritubercular Theory, while the actual appearances of the post-canine series in the Eocene mammals *Dissacus* and *Mesonyx* (figured by Wortman) provide substantial and impressive evidence in its favour. Professor Osborn admits this¹, yet he endeavours to rebut it not directly, but by adducing evidence to shew the "internal" position of the primitive cusp in an early mammal (*Dryolestes*). The premolar analogy theory demands a more thorough refutation than this.

B. The theory of Multituberculism or Polybuny. Some of the earlier opponents of Cope's theory are ranged on the side of

¹ *Evolution of Mammalian Molar Teeth*, 1907, pp. 217 et seq.

Forsyth-Major, who (*Proc. Zool. Soc.* 1893), for Rodents, proposed the alternative theory known as that of Multituberculism or Polybuny. Forsyth-Major is able to point to the facts (a) that in the *most ancient* of the fossil mammals (Fig. 208) the molar teeth are not tritubercular, but multitubercular, i.e. furnished with many small cusps¹; (b) that the Prototheria, which include the *most primitive*



Fig. 208. To the left. Two upper molar teeth of *Ornithorhynchus*. To the right. A molar tooth of *Microlestes moorei*. (After Thomas and Osborn.)

of known mammals (whether recent or fossil), the teeth are also of multitubercular type. Fossil remains of animals clearly ancestral to the existing Prototheria are not definitely known. One fossil form with characters suggestive of such a relation is *Tritylodon* (Jurassic), with multituberculate molar teeth. According to this theory the evolution of molar teeth has involved the loss of cusps

¹ The multituberculate form *Microlestes* is of Upper Triassic antiquity, whereas the most ancient trituberculate form, viz. *Amphitherium*, is of Mid-Jurassic antiquity only.

in most instances, and thus the position is diametrically opposed to that of Cope. Forsyth-Major was able to shew however that the history of the teeth of Rodents gives good support to his view, and Tims (*op. cit.* p. 139) confirms this application (of the theory) to Rodentia.

Considerations of the following kind are adverse to the multitubercular theory: (a) Should the "mammalian" claims of the Upper Triassic fossil remains known as *Dromatherium*¹ (Fig. 204, No. 3) be made good, then the multituberculate forms are coeval with a primitive "triconodont" form of molar tooth. From the latter type it is possible though not probable that the tritubercular types are derived. (b) Mammalian embryology shews that the cusps in development first assume a triangular disposition, whereas on the theory of Polybuny a multituberculate stage would be expected².

In so far as the Primates are concerned, the theory of Multituberculism is not easily applicable. Indeed the molar teeth of the Orang-utan, as well as occasional but not rare anomalous forms of the human molars (especially those of the lower set), suggest that the multitubercular condition may appear suddenly and sporadically. But it is not necessarily atavistic or reversionary, for it may imply adaptation to some special circumstances of nutrition.

C. The Theory of Concrecence. Another view is that of Tims (*op. cit. passim*), who was impressed with the fact that the cingulum is capable of throwing up offshoots in the form of cusps. This fact is duly recognized by the exponents of the tritubercular theory both as regards the premolar, and to some extent as regards the molar teeth. Tims proposes to adopt this explanation as regards the premolar teeth, while as regards the molar teeth, and this is an important point, he suggests the concrecence of primarily distinct elements placed originally in an antero-posterior

¹ This extraordinary animal is represented by a mandible, in which three incisors, a canine, three conical premolars, and seven molars are differentiated. The molars bear three conical cusps and are neither multituberculate nor trituberculate.

² Osborn, *Evolution of Mammalian Molar Teeth*, 1907, p. 208, deals in some detail with the theory of multituberculism.

sequence¹. Antero-posterior concrescence is the keystone of Tims' theory as regards the molar teeth, and it must be admitted as unfortunate that the evidence of concrescence is not yet convincing, except in *Sphenodon* (a reptile), in *Ceratodus* (a Dipnoan fish)², and perhaps in the Wallaby (a Marsupial), as suggested lately (1911) by Tims and Hopewell Smith.

Concrescence indeed has been assigned, as a name, to a definite theory, which would seem (cf. Marett Tims, *J. A. P.*, Vol. xxxvii. p. 134), to have been first advanced by Gervais. Its chief advocates in later years have been Röse and Kükenthal, against whom we may set Leche (*Bibl. Zool.* Heft 17, pp. 154, 155). The theory postulates the possibility of primitive conical dental elements fusing to form complex teeth: and the elements which thus fuse may belong to one and the same, or to different dentitions.

Röse (*Anat. Anz.* vii. p. 395) declares himself an advocate of the Concrescence theory as accountable for the origin both of premolar and molar teeth, and has represented his views in an elaborate diagram. It may be noted in conclusion of this brief notice, that Röse postulates the original presence of from 46—52 single conical teeth, which by fusion have constituted the dentition actually found in the Hominidae. Such a number of conical teeth is submitted to be not by any means unusual in the dentition of reptiles.

D. The Plexodont theory of Ameghino can only be mentioned here. It postulates the concrescence of primitive conical teeth in groups of four, with the production of compound four-cusped teeth. Further details are given by Osborn (*op. cit.* 1907, pp. 201 *et seq.*).

The foregoing notes contain an attempt to set forth in the most concise manner the several views which have been taken, and the hypotheses which have been advanced in explanation, of what is undoubtedly a difficult problem, and one upon which much light remains to be shed.

¹ In the Primates and most Eutheria, concrescence of pairs of such elements is suggested, while in the Elephants a greater number of elements would appear to have been fused together.

² But not in Protopterus, another Dipnoan fish (cf. Röse, *Anat. Anz.* vii. p. 399).

The tritubercular theory has been discussed at greater length than the other views, partly because of its special applicability to the Hominidae, and also because of the very important inferences based upon this by Cope and set forth by him in the *American Naturalist* (1893), and again, at a later date, in the *Primary Factors of Organic Evolution* (1896).

The molar teeth are the special object of study, and Cope and Topinard agree in declaring that the Hominidae, and especially the more highly civilized among recent Hominidae, are tending by reversion towards the condition of trituberculy in the upper molars, the hypocone (cf. Fig. 207, "PI") tending to disappear. Topinard (*L'Anthropologie*, 1892) gives some striking statistics from a research on several hundred crania, and has drawn up comparative tables illustrative of the tendency in the several human races (cf. also Tomes' *Dental Anatomy*, 1914). Both Topinard and Tomes appear to ignore the earlier work of Zuckerkandl and Röse (cf. Chapter XIV). Tomes (*op. cit.* p. 597) gives a very instructive tabulated statement illustrating Keith's researches into the relative degree of cusp development in the European and the Negro races, as well as in the higher apes.

This tendency to trituberculy (which is undoubtedly demonstrable) is considered by Cope¹ justification for the inference that the Hominidae and Simiidae have descended directly from Lemurine ancestors, to the exclusion of a "Cercopithecus stage" in the genealogical history of these two families. (This inference is not endorsed here.) Extinct Lemurs are appealed to, especially the small animal known as *Anaptomorphus* (cf. Chapter XVII.), whose nearest living relative is the very primitive *Tarsius* (cf. Chapter II.); also the various representatives of the Genus *Adapis* (cf. Chapter XVII.) which command a special interest in view of the features of their lower incisor teeth.

As was mentioned in the descriptive notes on the teeth of the Lemuroidea, the true Lemurs are distinguished by the very peculiar procumbent position and the extraordinarily styloid shape of their lower incisor and canine teeth. The possession of this character would be an obstacle to the acceptance of the view postulating the appearance of such Lemurine forms in the ancestry

¹ Haeckel and Klaatsch seem to be in agreement with Cope upon the general accuracy of this account.

of the Hominidae. The character has not been lately acquired, for the giant extinct Lemurs possess it (cf. Chapter xvii.), and it is worthy of remark that the same incisor form is found in the early Triassic Reptilia. But Cope (*Am. Nat.* 1893) was able to shew that several of the extinct Adapidae possessed a more generalized conformation in regard to the teeth in question. The typical Lemurine conformation is regarded as the result of adaptive specialization, and is not shewn by the Middle Eocene form of Lemur designated *Notharectus* (Gregory 1913). The condition of the lower incisors in the Lower Eocene form *Anaptomorphus* is obscure.

From the small Eocene American Lemuroids, Cope considered that a transition is easily demonstrable to extinct Eutherian groups known respectively as the Condylarthra (a parent ungulate stock)¹, or even to the Creodonta (ancestral carnivorous forms). The possibility of re-tracing the evolution of the Primates to the Creodonta is of great importance. For Cope held that the Creodonta were in turn derived from ancestors of a very primitive Marsupial or Metatherian (polyprotodont) type. Forsyth-Major (*Proc. Zool. Soc.*, 1893) and Marett Tims strenuously oppose this view, while Professor Gregory in 1913² recognizes the close affinities of the early Creodonts with the early Insectivora. In Gregory's opinion their distinction and separation must have occurred long before the beginning of the Tertiary period. In view of the recent extension of knowledge in regard to the anatomy and dentition of the Insectivora, it is now unnecessary to introduce the Creodonta into the ancestral line of the Primates, and reference to the scheme published by Dr Gregory (cf. Fig. 11 *supra*) shews the relative positions to be assigned on modern evidence to the Primates, Insectivora and Creodonta respectively³. The dental evidence is weighty on the side of confirming that scheme and the

¹ Cf. Osborn, 1907, p. 168.

² *Bulletins of the American Museum of Natural History*, Vol. xxvii. p. 307.

³ The sequence for the Primates given by Schlosser in 1911 is as follows (cf. Gregory, *Bulletins of the Geological Society of America*, Vol. xxiii. June 1912).

Hominidae (recent).

Simiidae (recent).

Pliopithecus (Pliocene).

Propithecus (Upper Eocene or Oligocene).

Parapithecus (Upper Eocene or Oligocene).

Tarsiidae (recent).

Anaptomorphidae (Lower Eocene).

ancestry of Man is traceable through Lemuroids and primitive Insectivora¹ backwards to the Mesozoic Placentalia², and Permian forms of which the Cynodont fossils fortunately enable us to gain an idea. In the later, i.e. the "post-Lemuroid," stages, forms comparable to those of the Cebidae, Cercopithecidae and Simiidae made their appearance. In regard to the two former families, the evidence of the dentition is not so clear as in the case of the latter, more especially the Chimpanzee.

The problem of the causation of different dental forms in various regions of one and the same jaw has been mentioned already. The exponents of the Tritubercular theory have always laid stress on "mechanical conditions" as accessory to functional adaptation (cf. Cope, *Primary Factors*, pp. 319 *et seq.*). Certainly the mechanical conditions will differ widely in different parts of the jaw; it is suggested that whereas the primary need was originally prehension, and that the crocodilian or cetacean types of dentition provide good examples of this; it is urged that with the acquisition and development of the habit of masticating food (whether like a primitive insectivore in crushing the scaly coats of its prey, or a primitive ungulate in reducing vegetable matter to pulp, or again in the habit of shearing flesh from bone as shewn by Carnivora), specialization and adaptation were associated in that section of the dental series at which power could be most advantageously applied; it is submitted that the comparative simplicity of the anterior teeth is contingent upon the retention of the prehensile function by this portion of the dental arcade.

And finally, when the Hominidae are considered, the interpretation thus advanced is found to apply to them just as to other Eutherian mammals, with the special qualifications introduced by the factor to which reference has been so often made, viz. the peculiar degree of reduction of the human jaws and the concomitant limitation of their functions.

¹ Cf. Matthew, *Bulletin of the American Museum of Natural History*, Vol. xxxi. pp. 307—314.

² In a private communication (March 28, 1914) Professor Gregory inclines to the view "that the ancestral Placental mammals were not minute exclusively insectivorous forms, but small sub-carnivorous animals, with stout zygomatics, sharp wedge-like upper molars, and with a talonid basin in the lower molars."

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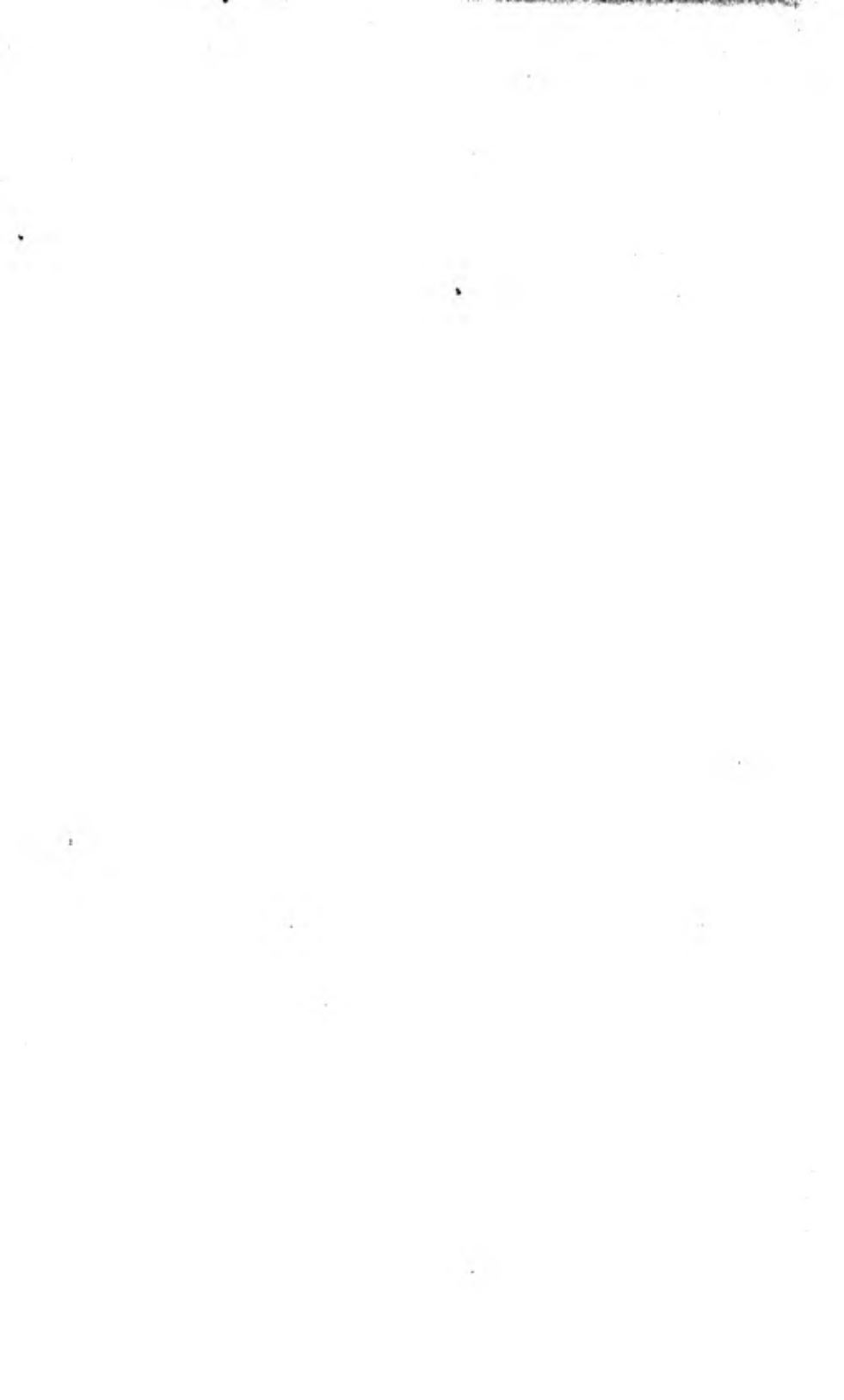
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